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# JOURNAL OF PALEONTOLOGY

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VOLUME 31 NOVEMBER, 1957 NUMBER 6


## PERMIAN AMMONOIDS FROM SOUTHERN ARABIA


A. K. MILLER AND W. M. FURNISH
State University of Iowa, Iowa City, Iowa



ABSTRACT—Single representatives of two ammonoid species are described from the Middle Permian near Haushi, Oman: *Pseudohalorites arabicus*, n.sp., and *Metalegoceras hudsoni*, n.sp. The former resembles congeneric specimens from central Hunan, China. The second is related to typical *Metalegoceras*, known from Artinskian-Leonardian strata in various parts of the world. The family Pseudohaloritidae is established for three Permian and Pennsylvanian ammonoid genera.


LATE in 1955 and early in 1956, Dr. R. G. S Hudson sent us for study a variety of cephalopods from Haushi and Wadi Lusaba, Oman, in the southeastern part of the Arabian Peninsula (21° 0.23′ latitude, 57° 36.2′ longitude). These fossils collected under the direction of Mr. D. M. Martin were found in a diversified fauna consisting of brachiopods, bryozoans, pelecypods, gastropods, trilobites, and ostracodes. The enclosing matrix is a limestone which is in part crinoidal. All came from the same general area in an 800-foot section of Permian conglomerates, sandstones, marls, and thin limestones, below Jurassic carbonates.

There was no obvious age assignment to be made from the original collection of fossil cephalopods in Oman, which consisted of only nautiloids and an aberrant ammonoid, *Pseudohalorites*. Subsequently, a representative of another ammonoid genus, *Metalegoceras*, was found in the same outcrop area, and it fixed the age of the fauna as early Middle Permian (Artinskian). Since that time, Chao's recent researches became available to us, and he had determined that typical *Pseudohalorites* of Hunan, China, is likewise Middle Permian. His conclusions were based largely on associated flora; the corroborative evidence from Oman is welcome.

Permian strata have long been known to occur in the southeastern portion of the Arabian Peninsula (Lees, 1928, p. 593–595). Various fossils, including *Richthofenia* and *Neoschwagerina*, were listed, but no ammonoids have been reported previously. Permian limestones several hundred feet thick are exposed in the Ras Musandam area of Hormuz Strait, and farther south in the Jebel Akhdar escarpment, west of Muscat. These previously listed Permian localities are considerably north of Haushi. Permian is also known from the interior of Saudi Arabia, Province of Nejd (Bramkamp et al. 1956); the Khuff limestone there has yielded nautiloids and brachiopods, but no ammonoids.


We are indebted to the Iraq Petroleum Company for permission to publish an account of these important Oman ammonoids. Dr. R. G. S. Hudson instigated this research, facilitated all arrangements, and transferred material and information. Dr. Roland

Goldring of the University of Bristol has prepared a study of the associated trilobites, and he has provided us with advance information on the results of his findings.

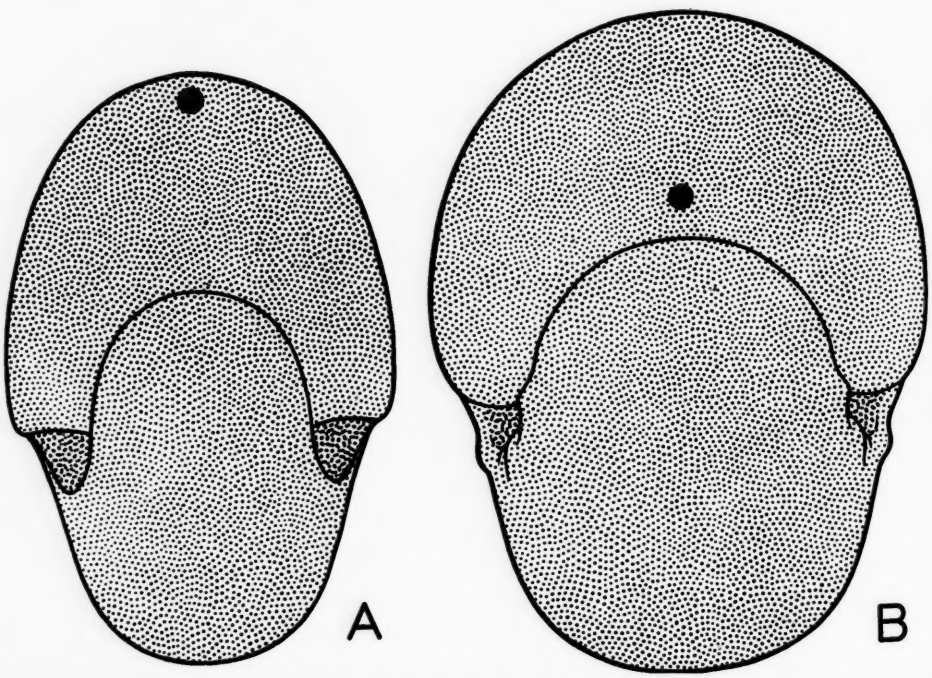
Family PSEUDOHALORITIDAE
Miller & Furnish, n. fam.

This family includes only a few inconspicuous forms of the Pennsylvanian and Permian: *Maximites*, n. gen., of the Middle Pennsylvanian; *Neoaganides* Plummer & Scott of the Upper Pennsylvanian-Middle Permian; and *Pseudohalorites* Yabe of the Middle Permian. Most are small and, probably as a result, appear to be rare. Conchs are globular to subdiscoidal with small or closed umbilici.

A characteristic familial feature is the aberrant position of the siphuncle. In the type genus, it is located fairly close to the dorsum—within the dorsal lobe but not marginal. *Neoaganides* has a siphuncle near a median position between the dorsum and venter, whereas in *Maximites* this feature is ventral but not marginal. One significance of an eccentric siphuncle in this group is a furthering of relationships otherwise apparent. There is no direct link between these Late Paleozoic forms and the Upper Devonian clymeniids, a group that stabilized the position of the siphuncle on the dorsum. Similarly, representatives of *Agathiceras*, in the Pennsylvanian and Permian, show a siphuncle median during early growth stages though marginal at maturity. All of these forms (as well as those in the Mesozoic with such an irregularity) are, in other respects, normal ammonoids, not directly related to each other.

The lobes of the external sutures are typically serrate in *Pseudohalorites* but are rounded in *Neoaganides*. The ventral lobe is distinctive in *Maximites*, for its distal portion is bifid; otherwise it is similar to *Neoaganides*.

Presumably, this family was derived from the Imitoceratidae of the Upper Devonian and Lower Carboniferous. The general




TEXT-FIG. *1*—Outline ventral views of *Maximites* and *Pseudohalorites*. *M. cherokeensis* (Miller & Owen) based on a syntype (State Univ. Iowa, 13484) from the Middle Pennsylvanian of Henry County, Missouri, ×20; and *P. subglobosus* Yabe based on a topotype? (State Univ. Iowa, 5991) from the Middle Permian of Hunan, China, ×4.

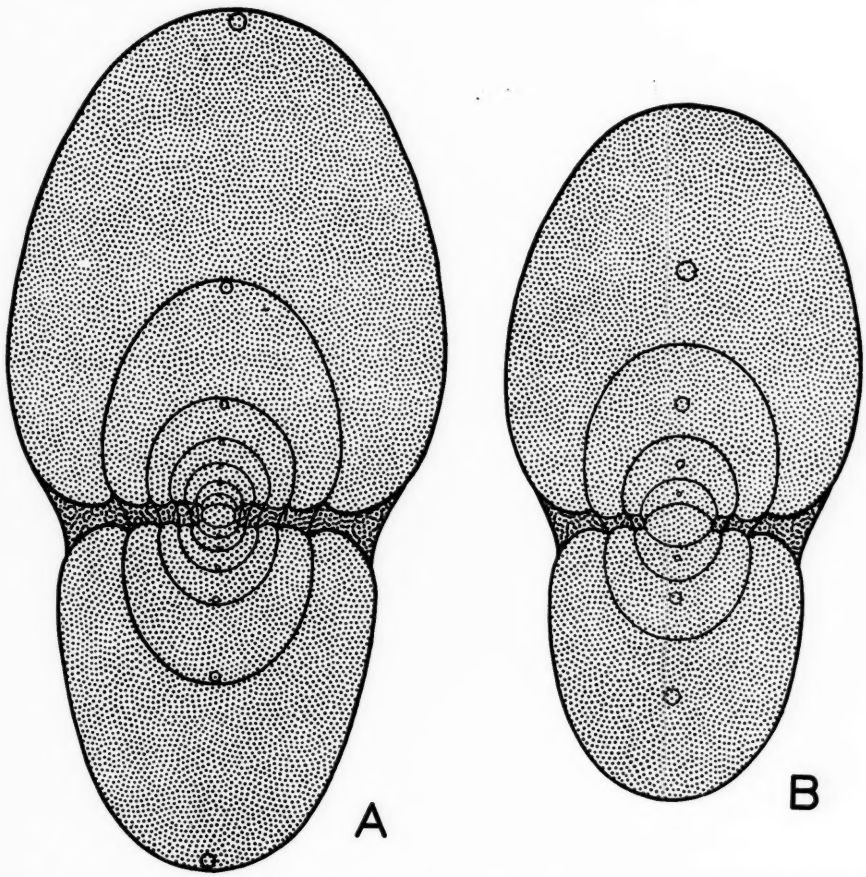
form of the conch, structure of the siphuncle, shape of the growth lines, length of the body chamber, and number of sutural elements are all comparable. Evolution from the Lower Carboniferous apparently involved a decrease in size, a change in the position of the siphuncle, and modifications in the nature of the mature aperture. Another possibility is that the ancestral form was a goniatitid in which the ventral lobe of the sutures became simplified; such a development might well have followed a decrease in size.

As others have noted, no descendants are known. The haloritids and comparably simple forms of the Middle and Upper Triassic appear to have evolved independently.

Genus MAXIMITES Miller & Furnish, n. gen.

Type species: *Imitoceras cherokeense* Miller & Owen.

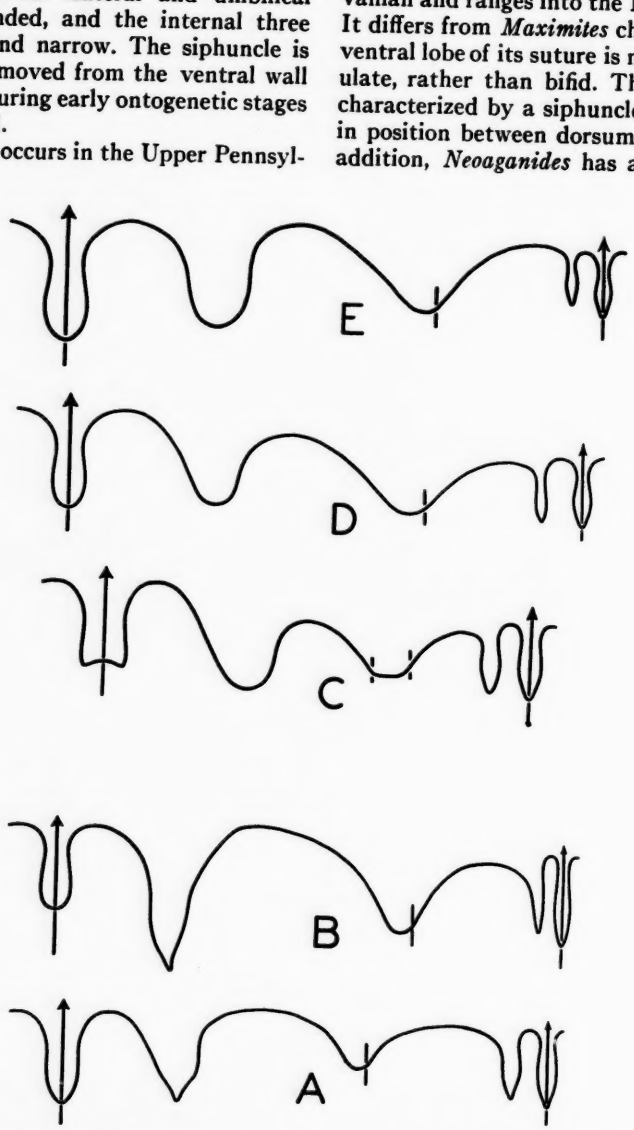
This genus is proposed for small Middle Pennsylvanian ammonoids related to *Neoaganides* Plummer & Scott. The conch is subdiscoidal and attains a diameter of about 10 mm. The venter is rounded, and the test is smooth except for faint spiral markings and biconvex growth lines. The umbilicus is small. At maturity, rather prominent ventrolateral lappets flank a hyponomic sinus. Each suture forms a total of 4 pairs of lobes, the ventral one of which




TEXT-FIG. 2—Diagrammatic cross sections of *Imitoceras* and *Neoaganides*. *I. ixion* (Hall) from the Lower Mississippian of Rockford, Indiana, ×5; and *N. pygmaeus* (Gemmellaro) from the Middle Permian of the Sosio Valley, Sicily, ×15. Based on topotypes: State Univ. Iowa, 13974, and U. S. Nat. Mus.

is distinctly bifid. Lateral and umbilical lobes are rounded, and the internal three are grouped and narrow. The siphuncle is appreciably removed from the ventral wall of the conch; during early ontogenetic stages it is subcentral.

*Neoaganides* occurs in the Upper Pennsylvanian and ranges into the Middle Permian. It differs from *Maximites* chiefly in that the ventral lobe of its suture is narrow and spatulate, rather than bifid. This genus is also characterized by a siphuncle nearly median in position between dorsum and venter. In addition, *Neoaganides* has a more strongly




TEXT-FIG. 3—Mature sutures of *Imitoceras*, *Maximites*, and *Neoaganides* in stratigraphic order.

(A) *Imitoceras* cf. *I. intermedium* Schindewolf. A specimen (State Univ. Iowa, 5975) from the Upper Devonian (Zone IV) 7 km. northwest of Beni Abbès, Algeria, at a diameter of 13 mm., ×4⅓.

(B) *I. ixion* (Hall). A topotype (State Univ. Iowa, 13974) from the Lower Mississippian Rockford Limestone of Indiana, at a diameter of 40 mm., ×1⅓.

(C) *Maximites cherokeensis* (Miller & Owen). A syntype (State Univ. Iowa, 13484) from the Middle Pennsylvanian Cabaniss Group, Henry County, Missouri, at a diameter of 4 mm., ×13.

(D) *Neoaganides grahamensis* (Plummer & Scott). A specimen (State Univ. Iowa, 5974) from the Upper Pennsylvanian Graham Formation near Jacksboro, northcentral Texas, at a diameter of 3 mm., ×20.

(E) *N. pygmaeus* (Gemmellaro). A topotype (U. S. Nat. Mus.) from the Middle Permian Sosio Limestone, Province of Palermo, Sicily, at a diameter of 5 mm., ×10.

modified apertural margin at maturity (Pl. 131, fig. 6,7). The "runzelschicht" (Pl. 131, fig. 4,5) is rarely preserved, and its nature is probably of no more than specific importance.

*Imitoceras* Schindewolf is one of the more abundant genera in the late Devonian and Lower Mississippian; though it probably occurs also in the Upper Mississippian. In contrast to the small *Maximites*, representatives are of moderately large size and attain a diameter of as much as 100 mm. In addition, the siphuncle is ventral and marginal in position. Also, there is a slight difference in the early ontogenetic development of these two genera; the prosuture of *Imitoceras* shows a ventral lobe, whereas that of *Maximites* has a simple rounded ventral saddle.

The small ammonoids referable to *Maximites* and *Ueoaganides* have often been overlooked or associated with immature specimens of other genera. However, their closely crowded septa and modified apertures clearly establish that the ultimate size had been attained. As early as 1888, Gemmellaro recognized and described, as *Brancoceras pygmaeum*, such a Permian representative from Sicily. His account was incorporated in an appendix to the classic report, and the species is presumed to have been overlooked originally. Maxim K. Elias collected specimens of comparable minute forms in the Pennsylvanian and noted their unique nature in 1934—his conclusion was not published, but the name *Maximites* is given in recognition.

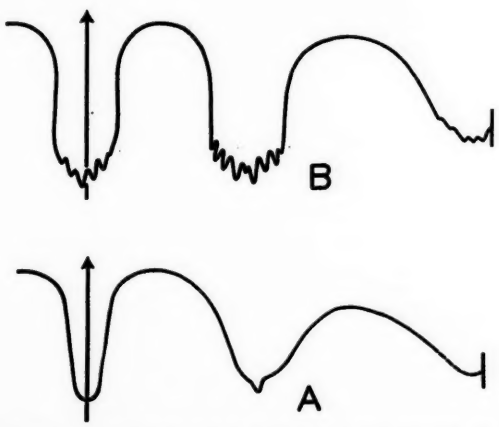
## Genus PSEUDOHALORITES Yabe, 1928

Type species: *P. subglobosus* Yabe, 1928.

*Pseudohalorites* YABE, 1920, Geog. Res. China 1911–1916, Atlas foss., pl. 19 [*nom. nud.*]; ——, 1928, Jap. Jour. Geol. Geog., Trans., vol. 6, p. 19–22, pl. 6; KUTASSY, 1933, Foss. Cat., Animalia, Pars 56, p. 629; SPATH, 1951, Cat. foss. Ceph. Brit. Mus., Pt. 5, p. 111; CHAO, 1954, Acta Palaeont. Sinica, vol. 2, p. 16–18, 46–50; KUMMEL, 1957, Treat. invert. paleont., Pt. L, p. 176.

*Hunanites* CHAO, 1940, Jour. Paleont., vol. 14, p. 71–73, pl. 10; SCHINDEWOLF, 1941, Palaeont. Zentralbl., p. 237; MILLER & FURNISH, 1957, Treat. invert. paleont., Pt. L, p. 50.

The conch is globular to subglobular with a closed umbilicus. There is a series of transverse ribs which branch near the umbilical borders. At maturity, the conch attained a diameter of some 40 mm. and developed a conspicuous apertural constriction. The body chamber is about a volution in length. Each suture forms 4 pairs of lobes, as is characteristic of the family. One of the most diagnostic features of the genus is the serrate nature of the external lobes, reminiscent of a parallel development in the Thalasso-




TEXT-FIG. 4—Mature external sutures of *Pseudohalorites* from the Middle Permian of central Hunan, China, showing extremes of development in associated forms.
(A) *P. celestris* Yabe. A topotype? (State Univ. Iowa, 5990) at a diameter of 15 mm., ×5.
(B) *P. subglobosus* Yabe. The type species, based on a topotype? (State Univ. Iowa, 5991) at a diameter of 16 mm., ×5½.

ceratidae. Such a feature is generally of fundamental importance in ammonoid classification but in *Pseudohalorites* is extremely erratic and is asymmetrically developed. The siphuncle is within the septal flexure of the dorsal lobe.

Only three closely related species are known, all from the Middle Permian of Asia. The specimens upon which this genus was based came from an "unknown" locality in the "Triassic or Permian" of "Hsiang-tan-hsien," Hunan, China. Subsequently, Chao described the same form from this district in central Hunan, without knowledge of Yabe's earlier work, and assigned it to the Lower Carboniferous. Because of the unique nature of the genus, several authors have regarded it as an enigma. In 1954, Chao restudied the type and associated species and determined that they are Middle Permian in age. The cephalopods were found to occur below a coal series with a *Gigantopteris* flora equivalent to that of the Loping coal in the adjacent province, Kiangsi. The shales which carry *Pseudohalorites* are stated to correlate with the Kufeng shale of the Lower Yangtze Valley, the Yangsinian of South China.

The genus appears to be moderately abundant at the single general locality in Hunan Province, China. Late in 1955 we were sent a representative of this genus from southeastern Arabia. The associated fossils are indicative of the Middle Permian, rather than Lower Carboniferous as we had heretofore believed.

Middle Permian ammonoids are particularly well known. The hundreds of species described from the Urals, Mediterranean, Timor, Texas-Coahuila, etc., show little provincialism. The genus under consideration, *Pseudohalorites*, is one of the first ammonoids to suggest a distinct Tethyan fauna.

PSEUDOHALORITES ARABICUS Miller & Furnish, n. sp.
Pl. 131, fig. 8, 9

This species is based on a single specimen, which is largely testiferous. The phragmocone is about 23 mm. in diameter, and it attains a maximum width and height of conch of 16 and 13 mm. An apertural portion of the body chamber, which adheres to this holotype, shows that it was almost a volution in length and attained a diameter of some 15 mm. more than that of the phragmocone.

The conch is subglobular in shape and is evenly rounded ventrally. The surface bears fine growth lamellae and prominent ribs which are convex and almost directly transverse. Apparently, as in congeneric species, the hyponomic sinus becomes more prominent at full maturity by the development of ventrolateral lappets. Also, at that stage, an apertural constriction is present.

For the most part, the sutures are discernible only from the adoral septum of the holotype. The lateral lobes of the external suture are relatively shallow and are serrate; each appears to bear only a couple of serrations.

The siphuncle is about 1 mm. in diameter at the adoral end of the phragmocone, where the ventro-dorsal dimension is 7½ mm. The center of the siphuncle is about 2 mm. from the dorsum.

*Remarks.*—This form is similar to the type species of *Pseudohalorites*, *P. subglobosus*, but is less globular and has fewer serrations on the lobes of the sutures. It appears to be even more closely related to *P. celestris* Yabe from the same general horizon and locality as the type. Both of these Hunan species seem to be variable or unstable, and more nearly precise comparisons cannot be made from the available information.

On the holotype of *P. arabicus* there is a series of longitudinal lirae just outside the umbilical margin. These are visible at only one place on the surface of the test and may be adventitious.

*Occurrence.*—The light-gray limestone matrix is in striking contrast to the yellow-orange shell material of the holotype. The specimen is from one of a series of thin limestones near the top of the Permian section exposed at Haushi, Oman. A variety of fossils was found in direct association with it, but the only other ammonoid from this general locality, *Metalegoceras hudsoni*, n. sp., was secured somewhat lower in the section. The specimen was collected by D. M. Morton and Max Chatton of the Iraq Petroleum Co., Ltd.

*Repository.*—State Univ. Iowa, 8107.

Family METALEGOCERATIDAE Plummer & Scott, 1937

Genus METALEGOCERAS Schindewolf, 1931

METALEGOCERAS HUDSONI Miller & Furnish, n. sp.

Pl. 132, fig. 1–3

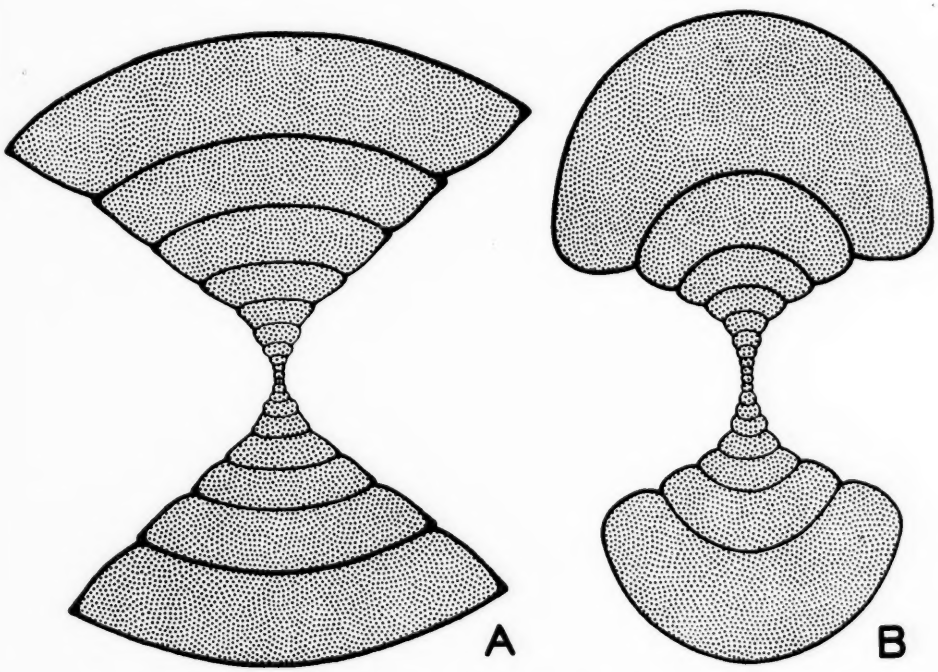
*Metalegoceras* aff. *clarkei* HUDSON, Geol. Soc. London, Proc., no. 1549, p. 74.

The only known representative of this species is a septate internal mold 38 mm. in diameter. The preserved part of its conch attains a maximum height of whorl of 19 mm. and a corresponding width of 27 mm. The diameter of the umbilicus is about a fourth that of the specimen. Except for indistinct transverse constrictions, the surface of the internal mold is smooth.

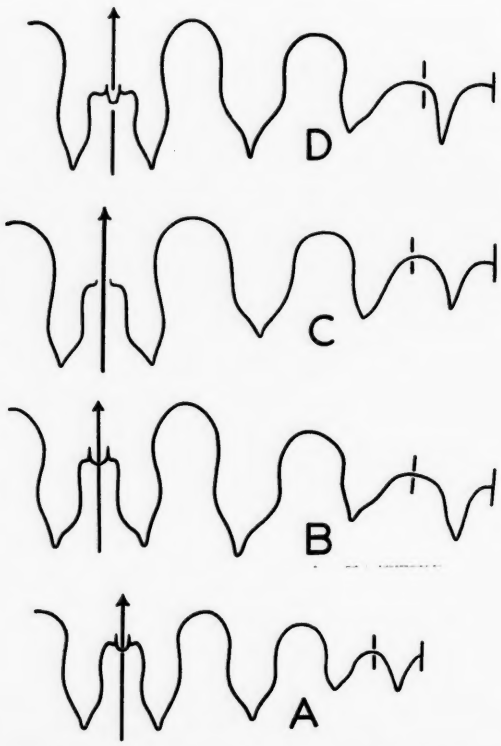
Traces of an outer volution which adhere to this specimen, indicate that the phragmocone formed another whorl. It attained an estimated diameter of about 65 mm., and the body chamber would have added another volution. This size is normal for the genus.

The shape of the external suture (Text-fig. 6B) is typical for *Metalegoceras*. Also, the internal suture is like that of comparable forms, and it consists of a narrow dorsal lobe, and two pairs of lanceolate dorsolateral lobes.

*Remarks.*—This species is closely similar to some from Timor and the Urals. The genus is abundantly represented in the Bitauni beds of Timor, the source of approximately 500 specimens, which have been studied by Haniel and J. P. Smith. In 1933, de Marez Oyens summarized the work and presented an analysis of relationships based on detailed measurements of 77 specimens. As might be expected, he was able to demonstrate gradational differences; the specimen under consideration represents an extreme within that range. It resembles the Timor form which has been known as *M. australe* (Smith). Also, it is similar to *M. tschernyschewi* (Karpinsky) of the Artinskian in the Ural region, which has a larger umbilicus. *M. clarkei* Miller of Western Australia and *M. baylorense* (White) of




TEXT-FIG. 5—Diagrammatic cross sections of two species of *Metalegoceras* from the Artinskian of the Urals: *M. sogurense* (Ruzhencev) and *M. tschernyschewi* (Karpinsky), about ×2. From Ruzhencev.




TEXT-FIG. *6*—Mature external sutures of Middle Permian *Metalegoceras*.
(A) *M. clarkei* Miller, The larger syntype from the Kimberley Division, Western Australia, at a diameter of 24 mm., ×2½.
(B) *M. hudsoni*, n. sp. The holotype (State Univ. Iowa, 5994) from Oman, at a diameter of 32 mm., ×2½.
(C) *M. evolutum* (Haniel). The type species from Timor, enlarged. After Haniel.
(D) A form from the Ural region referred to *M. evolutum* by Ruzhencev, at a diameter of 45 mm., ×2. From Ruzhencev.

Texas have proportions comparable to those of these several species.

*Occurrence.*—The matrix of this specimen is red argillaceous limestone with scattered sand grains. It came from the lower half of the Permian section near Haushi, Oman, the same general locality which yielded *Pseudohalorites arabicus* higher in the section. The holotype was collected by D. M. Morton and Max Chatton of the Iraq Petroleum Co., Ltd.

*Repository.*—State Univ. Iowa, 5994.

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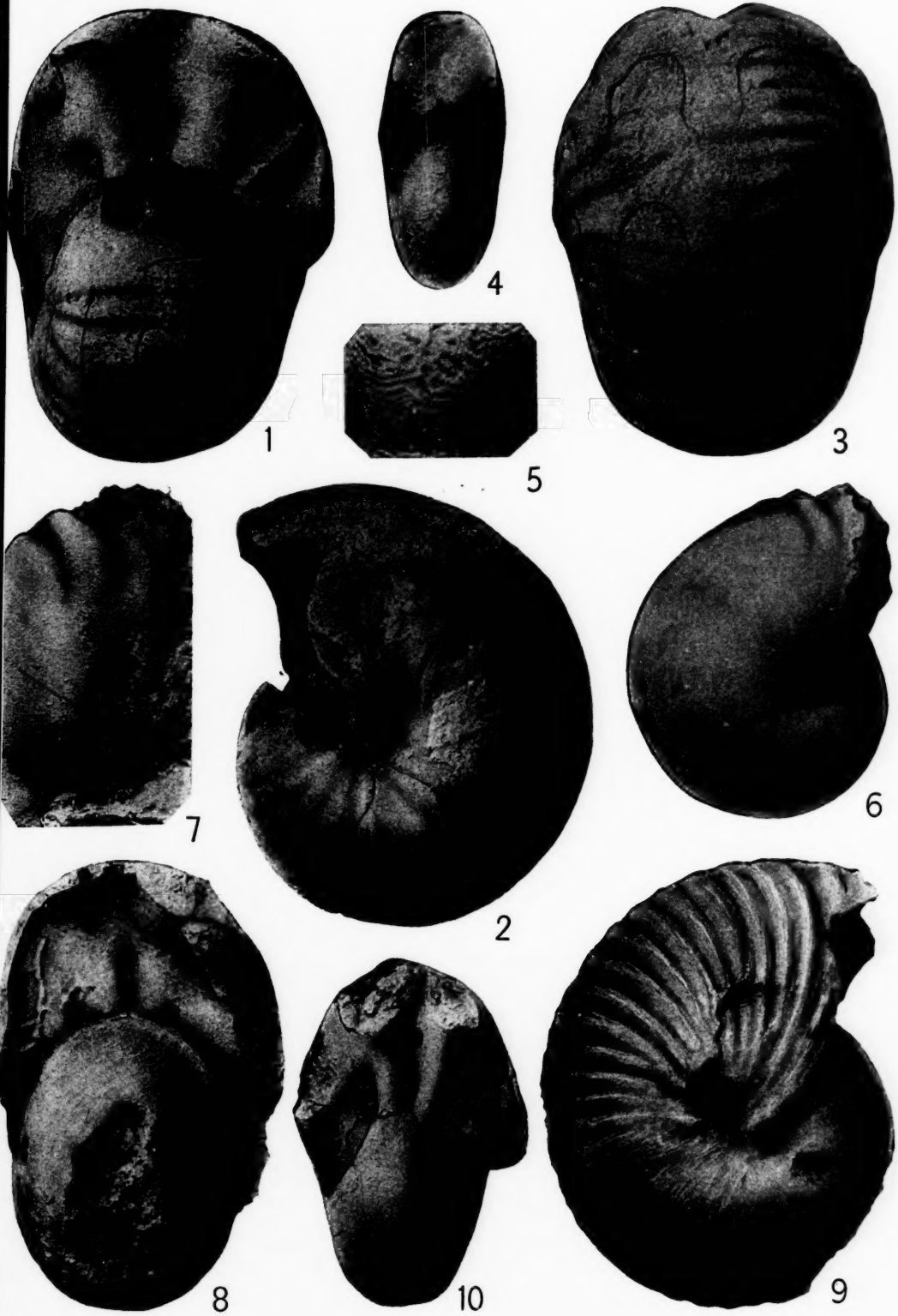
EXPLANATION OF PLATE 131

FIG. *1–3*—*Pseudohalorites subglobosus* Yabe. A topotype? (State Univ. Iowa, 5991) from Permian Shale below the Tanchiashan coal series, Hsiangtan District, central Hunan, China, ×3.
*4–7*—*Neoaganides pygmaeus* (Gemmellaro). Three topotypes (U. S. Nat. Mus.) from the late Middle Permian Sosio Limestone of Sicily; *4,6*, ×4½; *5*, ×10; *7*, ×7. *5*, An enlargement of ventral surface shown in *4*. *7*, Apertural portion of a specimen like *6*.
*8,9*—*Pseudohalorites arabicus*, n. sp. The holotype (State Univ. Iowa, 8107) from the early Middle Permian near Haushi, southern Arabia, ×3.
*10*—*Neoaganides multiseptatus* (Chao). A paratype (State Univ. Iowa, 8106) from same horizon and locality as *1–3*, ×3.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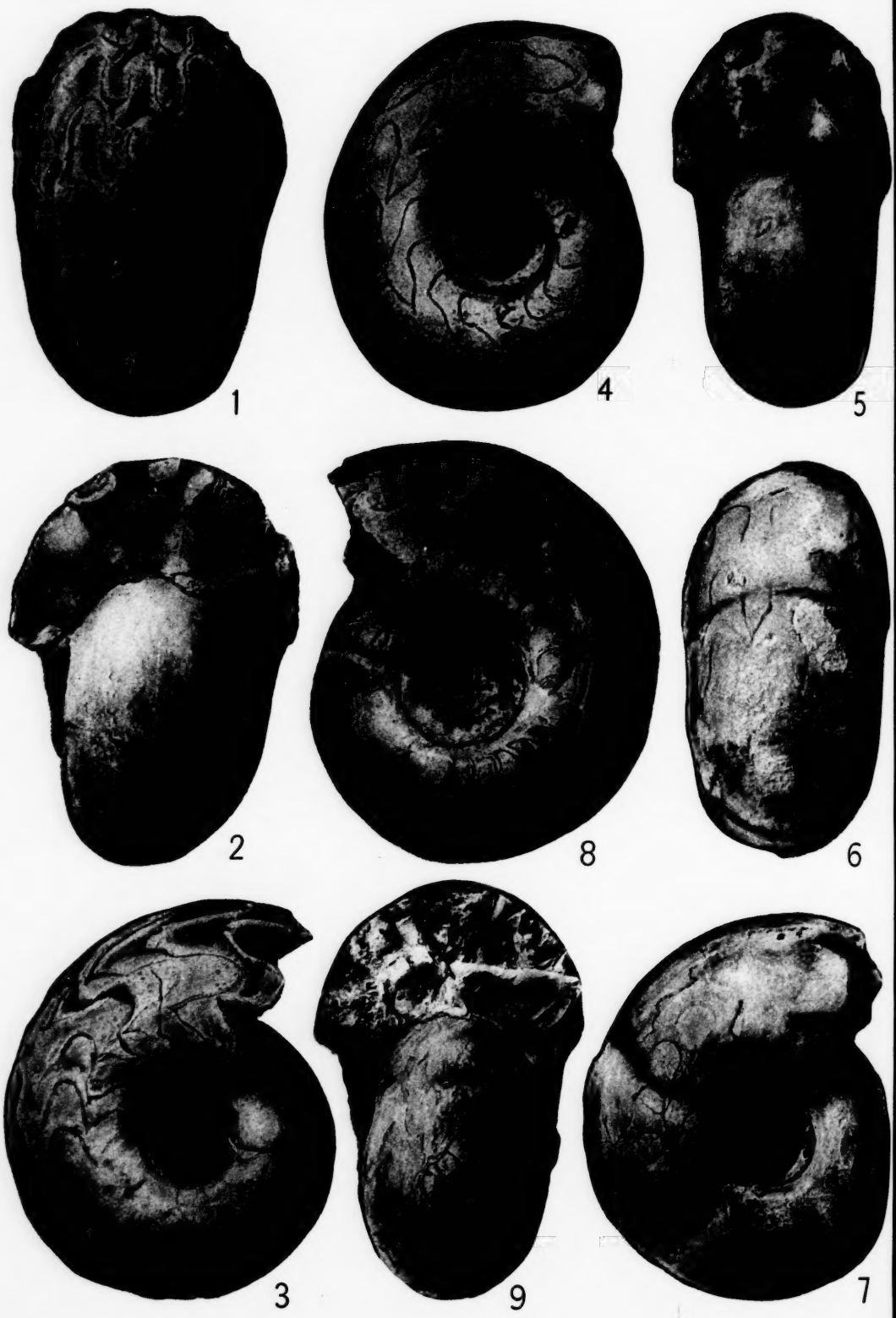
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## EXPLANATION OF PLATE 132

FIG. *1–3—Metalegoceras hudsoni*, n. sp. The holotype (State Univ. Iowa, 5994) from the early Middle Permian near Haushi, southern Arabia, ×1½.

*4—Metalegoceras baylorense* (White). A topotype from the upper Wichita Group, Baylor County, Texas, slightly more than ×1. After Plummer & Scott.

*5–7—Metalegoceras clarkei* Miller. The larger syntype from the early Middle Permian, Kimberley Division, Western Australia, ×2½.

*8,9—Metalegoceras tschernyschewi* (Karpinsky). A specimen (State Univ. Iowa, 5992) from the Artinskian of the Aktubinsk District, southern Urals, slightly more than ×1.

JOURNAL OF PALEONTOLOGY, VOL. 31, NO. 6, P. 1052–1056, 2 TEXT-FIG., NOVEMBER 1957

# AMMONOIDS OF THE BASAL WORD FORMATION, GLASS MOUNTAINS, WEST TEXAS

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ABSTRACT—Seven genera of ammonoids are known to be represented in the first limestone member of the Word Formation. The most significant are a typical *Perrinites*, characteristic of the underlying Leonard, and an unusual *Stacheoceras*, *S. normani*, n. sp. The latter is a pseudomorph and predecessor of *Waagenoceras*, distinctive of higher portions of the Guadalupian. Collectively, the ammonoids represent a combination of Leonard and Word elements.

THE extensive collections of Texas Permian ammonoids available for study before 1940 contained relatively few specimens from the lower portion of the Word Formation. Only poorly preserved individuals were then available to us; they appeared to be similar to those from younger beds, and we tentatively identified some immature ones as *Waagenoceras dieneri* Böse. Plummer & Scott in their well known monograph of the Upper Paleozoic ammonoids of Texas, listed the genera *Perrinites* and *Waagenoceras* as occurring together at this horizon, but we were reluctant to accept their conclusion for the collections we were studying failed to confirm it. Furthermore, we had not observed. *Perrinites* above the Leonardian. Wherever a sequence of Middle Permian ammonoid faunas had been known to occur (Texas, Coahuila, and Timor) there appeared to be a break between the Leonardian and Guadalupian.

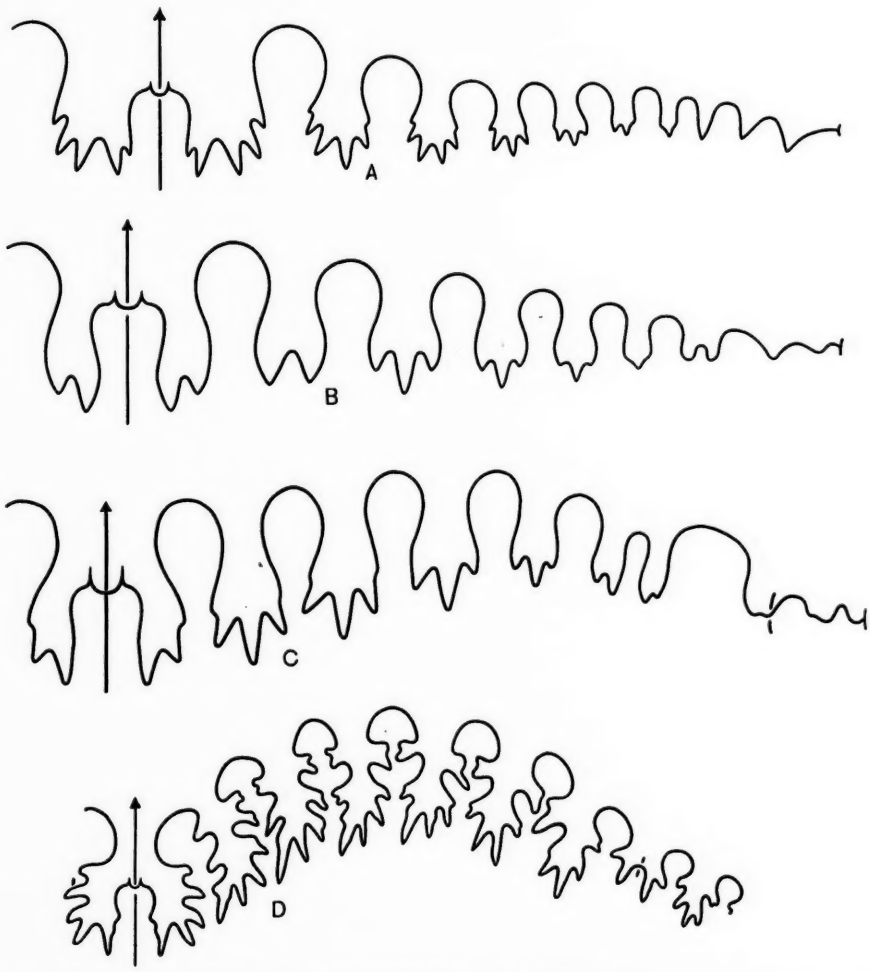
Later, after G. Arthur Cooper inaugurated his large-scale program of securing acid residues from the Permian limestones of West Texas, he found quite a number of well preserved specimens in unique occurrences. Among these was included a series of specimens from a limestone near the Leonard-Word boundary (Unit 1a of King's Section 24, 1930, p. 143). It yielded numerous representatives of *P. hilli* (Smith) and was questionably regarded as uppermost Leonard (Miller, 1945, p. 14). This collection also included two globular ammonoids which resembled *Waagenoceras dieneri* Böse but showed portions of the sutures that indicated a relationship to *Stacheoceras* (Miller, 1945, text-fig. 2, pl. 8, fig. 7, 8). The associated forms (*Adrianites*, *Pseudogastrioceras*, and *Medlicottia*) were not conclusive of either age.

Clifton (1945, p. 1774) called attention to the occurrence of *Perrinites* and *Waagenoceras* in association within the first limestone member of the Word. P. B. King (1947, p. 775) reviewed the work and concluded that both genera were here near the limits of their ranges, and that their stratigraphic significance was therefore not greatly affected.

More recently, Norman D. Newell has secured ammonoids in connection with his intensive studies of the West Texas Permian. One of his collections contains several well preserved representatives of *Perrinites hilli* and an exceptionally fine example of the elusive globular form from the first Word limestone. This specimen clearly displays all of the significant features; and its sutures reveal a relationship to those of *Stacheoceras* and *Waagenoceras*, as well as *Popanoceras*, but are relatively close to those of the first of these three (Text-fig. 1). Such differentiation is obscured by the fact that these genera are related, and it is believed that *Waagenoceras* evolved from *Stacheoceras* during early Word time. *Waagenoceras dieneri* passed through a *Stacheoceras* stage of development when the diameter of its conch was some 10–15 mm. *Stacheoceras gilliamense* Böse, probably a synonym of *W. dieneri*, was based on such immature specimens. The holotype of the Word globular *Stacheoceras* species is about 40 mm. in diameter and is therefore mature.

Other areas in this general region yield little or no confirmatory evidence. The Cutoff Member of the Bone Spring Forma-

tion in the Guadalupe Mountains has been studied by P. B. King and Norman D. Newell and their associates. Also, Walter C. Warren sent us a specimen of *Pseudogastrioceras* cf. *P. serratum* (Girty) from this member on the west side of the Guadalupes. A few miles to the north in New Mexico, Donald W. Boyd has collected several ammonoids from the lower San Andres equivalent of the Cutoff. Boyd's collection contains *P.* cf. *P. serratum* and good specimens of *Perrinites hilli*. Other San




TEXT-FIG. *1*—Mature external sutures of Middle Permian Cyclolobaceae.

(A) *Popanoceras bowmani* (Böse), based on a topotype (Yale Peabody Mus., 16819) at a diameter of 40 mm., from the third limestone member of the Word Formation near the junction of Road and Gilliland canyons, Glass Mountains, Texas, ×4.

(B) *Stacheoceras rothi* Miller & Furnish, based on a syntype (Yale Peabody Mus., 16817) at a diameter of 33 mm., from the Leonard Formation about 1 mi. southwest of Old Word Ranchhouse, Glass Mountains, ×4.

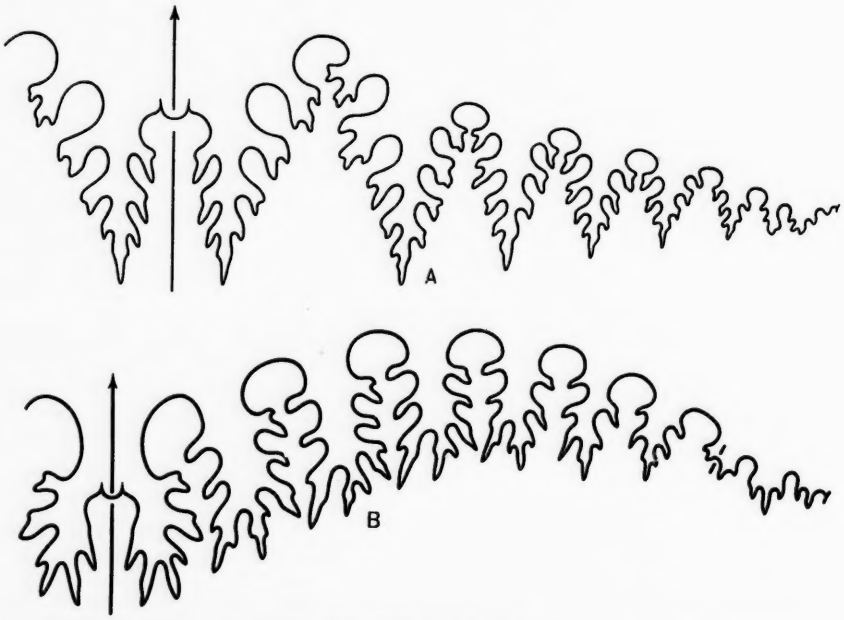
(C) *Stacheoceras normani* M. & F., n. sp., based on the holotype (Amer. Mus. Nat. Hist., 28022) at a diameter of 34 mm., from the first limestone member of the Word Formation just southwest of Old Word Ranchhouse, Glass Mountains, ×4.

(D) *Waagenoceras mojsisovicsi* Gemmellaro, the type species of the genus from the Sosio Limestone of Sicily, largely after Gemmellaro.

Andres localities are about 50–75 miles to the north, near Cloudcroft and west of Artesia. Also, from 75 miles farther west, Kottlowski et al. (1956, p. 61) listed *Perrinites* and *Pseudogastrioceras* in the upper San Andres of the northern San Andres Mountains. A globular ammonoid tentatively identified as *Waagenoceras* sp. (Newell et al., 1953, p. 23,232) was found a few miles south of El Capitan, the end of the Guadalupes, in what King had regarded as "southern Cutoff" but which Newell placed in the Brushy Canyon Formation at the base of the Delaware Mountain Group. Fossils are rare in this part of the section, and few identifiable specimens are known from the impure limestones and sandstones. In the Permian outcrop area of north-central Texas and western Oklahoma, some 300 miles to the east, *Perrinites hilli* has been found abundantly in several thin dolomites at various localities.

*Summary.*—The lower Word ammonoid fauna can be said to consist of seven genera: *Agathiceras*, *Perrinites*, *Stacheoceras*, *Adrianites*, *Pseudogastrioceras*, *Medlicottia*, and *Paraceltites*. Only the *Perrinites* and *Stacheoceras* are critical for differentiating zones within the Leonardian-Guadalupian. The former is a characteristic fossil of the Leonardian but in the Glass Mountains is almost equally abundant in rock of basal Guadalupian age—it has not been observed in younger strata nor in direct association with *Waagenoceras*. *Stacheoceras normani*, n. sp., established in this study for the enigmatic globular ammonoid, seems to be a good index for the basal Guadalupian; it is ancestral to *Waagenoceras*, with which it has been confused.

We are perhaps inclined to carry a prejudice by still favor interpretation of ammonoid zones as direct correlatives. The preponderance of evidence for placing the *Perrinites*-bearing "Blaine of Texas" and portions of the San Andres as high as middle Guadalupian (Skinner, 1946, and others) involves physical criteria with which we




TEXT-FIG. 2—Mature external sutures of *Perrinites* and *Waagenoceras*.
(A) *P. hilli* (Smith), based on a specimen (Yale Peabody Mus., 16719) at a diameter of some 100 mm., from the Leonardian of Valle de Las Delicias, Coahuila, ×1.
(B) *W. dieneri* Böse, based on a topotype (Yale Peabody Mus., 16824) at a diameter of 35 mm., from the third limestone member of the Word Formation near the junction of Road and Gilliland canyons, Glass Mountains, Texas, ×3.

are unfamiliar. Fusulinids from subsurface San Andres have been documented as Guadalupian.

STACHEOCERAS NORMANI Miller & Furnish, n. sp.
Pl. 133, fig. 7, 8

*Waagenoceras* sp., KING, 1930, Texas Univ. Bull. 3038, p. 139 [part]; ——, 1942, Amer. Assoc. Petrol. Geol., Bull., vol. 26, p. 659 [part]; ——, 1947, ibid., vol. 31, p. 775 [part]; MILLER & GARNER (*in* Cress et al.), 1953, West Texas Geol. Soc., Gdbk. 1953, p. 65 [part]; (?) NEWELL ET AL. (*fide* Miller), 1953, Permian reef complex . . . , p. 23, 232.

*Waagenoceras dieneri* PLUMMER & SCOTT, 1937, Texas Univ. Bull. 3701, p. 397 [part]; MILLER & FURNISH, 1940, Geol. Soc. Amer., Spec. Paper 26, p. 173 [part]; CLIFTON, 1945, Amer. Assoc. Petrol. Geol., Bull., vol. 29, p. 1770, 1774, 1775, 1776 [part]; ——, 1946, Jour. Paleont., vol. 20, p. 557.

*Stacheoceras* sp. MILLER, 1945, Jour. Paleont., vol. 19, p. 14, 18, 19, pl. 8, fig. 7,8; CLIFTON, 1945, Amer. Assoc. Petrol. Geol., Bull., vol. 29, p. 1770.

Over a period of years, a good many representatives of this species have been recorded, but no clear understanding of it could be achieved until recently when Norman D. Newell loaned us the specimen we are designating the holotype (Pl. 133, fig. 7, 8). The conch is nearly spherical; at a diameter of 41 mm. its width is 38 mm. The phragmocone of the holotype attains a diameter of about 40 mm., the same size as that calculated for two incomplete specimens collected and loaned to us by G. Arthur Cooper. Presumably the body chamber constituted another full volution, so the maximum overall diameter of the conch in this species was some 60 mm.

The umbilicus is moderately small, having a diameter of only about a sixth that of the conch. The umbilical borders are fairly distinct, and the umbilical walls steep.

Growth lines are indistinct but are almost straight and directly transverse. The internal mold of inner volutions has constrictions with a similar trend.

The external sutures form a large bifid ventral lobe and, on either side of it, six digitate lateral and auxiliary lobes (Text-fig. 1C). The fifth and six lobes dorsad of the ventral one are relatively small and are paired. The umbilical lobe is complex and consists of four distinct parts. The internal suture forms a prominently trifid dorsal lobe and a series of narrow digitate dorsolateral lobes, each of which is directly opposite a lobe of the external suture.

*Remarks.*—This species is distinctive of the basal portion of the Word Formation. The holotype and the available paratype came from acid residues, as did the paratype illustrated by Miller in 1945.

The proportions and general physiogomy of the conch are virtually identical with those of *Waagenoceras dieneri* Böse, which is characteristic of the second and third limestone members of the Word. In both of these species, the septa form the same number of inflections, and a distinction must be based on the secondary subdivisions of the lobes. In *S. normani*, as in other representatives of the genus, only the aboral portions of the lobes are digitate; whereas in *W. dieneri* comparable digits are present on the flanks.

The species under consideration resembles *S. bransonorum* Miller & Cline of the phosphate rock in the Phosphoria Formation near the Idaho-Wyoming boundary. However, both of the type specimens of that species are dwarfed and are estimated to have attained a maximum diameter of only some 20 mm. at maturity (as compared with 60 mm. in *S. normani*). Furthermore, *S. bransonorum* has a small protoconch and was small throughout ontogenetic development, even though at maturity the conch consists of 10 or so volutions, as does that of related popanoceratids. Some advanced representatives of *Waagenoceras*, which reached a diameter of 100 mm., had comparable sutures when the conch was the same size as that of the types of *S. bransonorum*—the syntypes of *S. gilliamense* Böse belong in this category.

*S. normani* and *S. bransonorum* are the only two markedly spheroidal representatives of *Stacheoceras* that have been described—both have a width-height ratio of about 2:1. *S. rothi* Miller & Furnish of the Leonard Formation in the Glass Mountains (Text-fig. 1B) is an average representative of the genus—it has a width-height ratio of 4:3. *Stacheoceras* occurs in various portions of the Guadalupian Series in Coahuila, but all are subdiscoidal with a width-height ratio of about 1:1. At a comparable size

*Popanoceras bowmani* (Böse) of the middle Word has a ratio of 1:2.

*Occurrence.*—The first limestone member near the base of the Word Formation yielded the holotype and two paratypes at a locality about half a mile southwest of the Old Word Ranchhouse, Glass Mountains, Brewster County, West Texas (U. S. Nat. Mus., Loc. 703—*see* Yochelson, 1956, p. 268). The exposure occurs on the northwest side of the road and near the top of the slope. R. E. King (Miller & Furnish, 1940) and R. L. Clifton apparently had specimens from the same ledge. In addition, the former collected material (believed to be conspecific) north of Leonard Mountain and in Gilliland Canyon, within the same general area of the Glass Mountains.

*Repositories.*—The holotype is Amer. Mus. Nat. Hist., 28022. The paratype illustrated by Miller in 1945 is U. S. Nat. Mus., 111630; an unfigured paratype and several small immature specimens are at the same institution. King's material, which we have studied, is at Yale Peabody Mus.

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JOURNAL OF PALEONTOLOGY, VOL. 31, NO. 6, P. 1057–1068, PL. 133–134, 6 TEXT-FIG., NOVEMBER 1957

# PERMIAN AMMONOIDS FROM WESTERN UNITED STATES

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ABSTRACT—All the known Permian material from the Great Basin and adjacent areas is considered. Representatives of *Properrinites*, *Crimites*, and *Daraelites* are described from the Wolfcampian of Nevada. From the Leonardian are recorded *Perrinites*, *Popanoceras?*, and *Pseudogastrioceras* in Arizona; *Pseudogastrioceras* in Utah; also *Perrinites* and *Spirolegoceras*, n. gen., in Idaho. An account of a new species of *Stacheoceras* from the Middle or Upper Permian of northern California is included.

IN THE region of the Great Basin, Late Paleozoic strata are extensively developed and well exposed. However, the only widespread ammonoid assemblage that they have yielded is Upper Mississippian in age, Pennsylvanian forms are entirely unknown, and Permian specimens are rare.

During the present study an effort has been made to locate and investigate every reported occurrence of Permian ammonoids in the states west of the Rockies. Results have been meager, but it is hoped that a summary will facilitate future work. Altogether, specimens are known from about a dozen widely separated localities. A few species have been described from the Phosphoria Formation in an adjacent area near the Idaho-Wyoming border; a new genus, *Spirolegoceras*, is established for a species, *S. fischeri*, not previously recorded from this vicinity. An equivalent of the Phosphoria fauna is reported from the Wasatch Mountains in central Utah. Southeastern Arizona has yielded Leonardian ammonoids at three localities. A few specimens have been secured from Wolfcampian rocks at three localities in northeastern Nevada 100 miles apart. Finally, from northern California we are describing an individual that has been known for more than 50 years.

Collections have been loaned for study by numerous individuals. Most of this material was secured in connection with projects sponsored by various oil companies. Acknowledgment is also due Allan Blizzard for work on our illustrations.

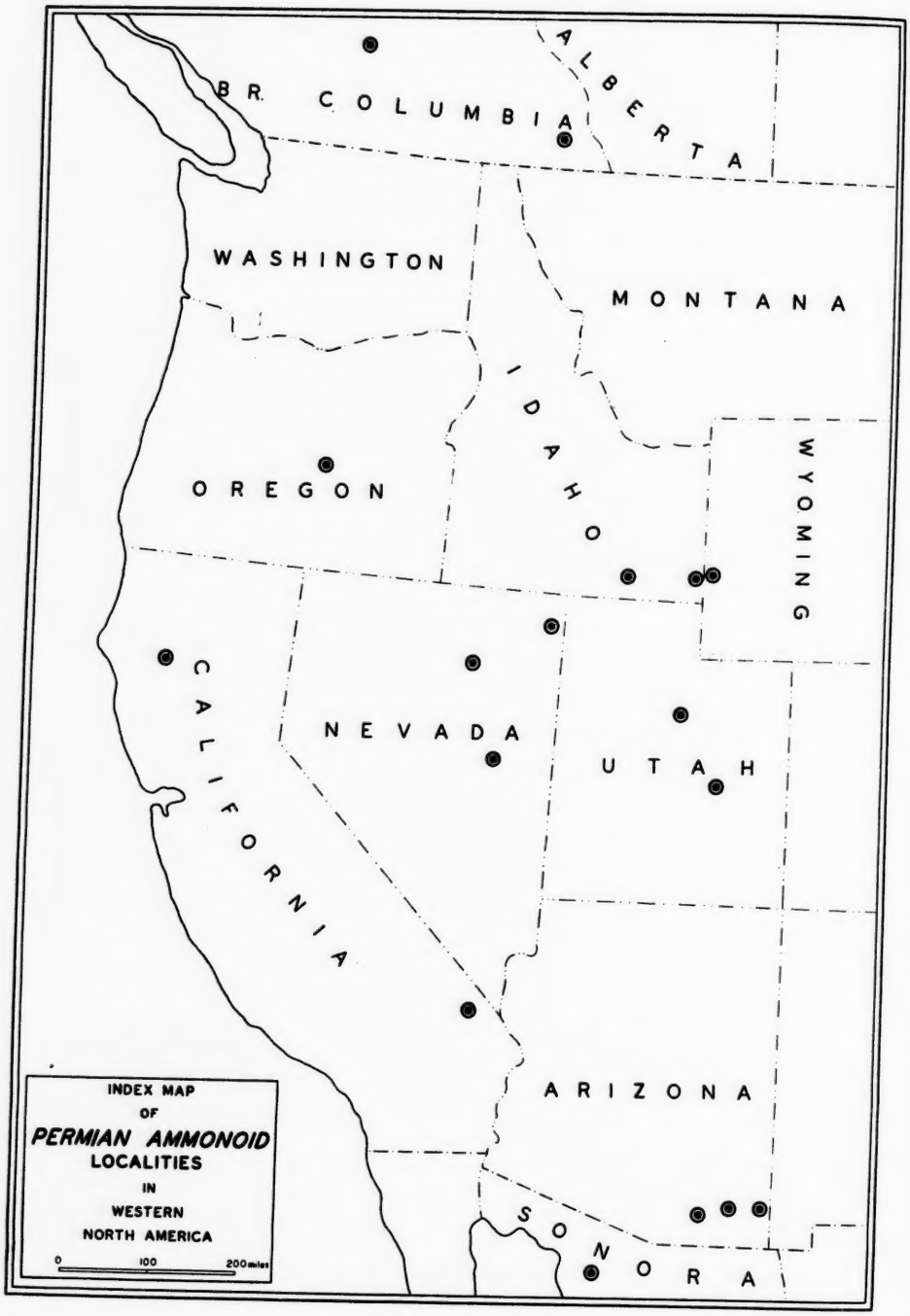
## FAUNAL DISTRIBUTION

Fusulinid and brachiopod assemblages are relatively well known in the Great Basin, and age determinations have generally been based on them. The American Permian brachiopods have been systematized particularly through the work of Dunbar, King, Cloud, and more recently Cooper and Stehli. Dunbar and Skinner's fusulinid studies in the West Texas sequence serve as a basis for reference. Similar faunas have been described by Thompson and associates from collections made in California, Nevada, Utah, etc. A variety of other fossils exist; Miller and associates have described several species of nautiloids from northern Arizona.

*Idaho-Wyoming.*—The only abundant Permian ammonoid fauna known from this entire region is that of the Phosphoria Formation in the Sublette Range of westernmost Wyoming. Practically all of the specimens are referable to a single genus, *Pseudogastrioceras*, but the following species are known from the Phosphoria in this general area:

*Peritrochia girtyi* (Miller & Cline)
*Stacheoceras bransonorum* Miller & Cline
*S. sexlobatum* Miller & Cline
*Pseudogastrioceras simulator* (Girty) [and varieties]
*Spirolegoceras fischeri* M., F., & C., n. gen, n. sp.

This fauna occurs in the Meade Peak phosphatic shale member, from which we have recovered several hundred specimens. *Spirolegoceras fischeri* was secured from near the top of the unit at a locality some 10 miles to the west of the Sublette Range. The age of this assemblage is thought to be Leonardian; *Spirolegoceras* is closely related to *Metalegoceras*, and the entire family Metalegoceratidae is restricted to the Wolfcampian and Leonardian. Normal representatives of *Stacheoceras* and *Pseudogastrioceras* are characteristic of Middle and Upper Permian


BR. COLUMBIA
ALBERTA
WASHINGTON
MONTANA
IDAHO
WYOMING
OREGON
CALIFORNIA
NEVADA
UTAH
ARIZONA
SONORA
INDEX MAP
OF
PERMIAN AMMONOID
LOCALITIES
IN
WESTERN
NORTH AMERICA
0
100
200 miles

TEXT-FIG. *1*

strata all over the world. Fusulinids of probable upper Wolfcampian age (Thompson, 1946, p. 8) are known from Phosphoria? strata in Montana. Williams (1956, p. 2857–2858) has indicated that there is a considerable range in age within the Phosphoria.

Almost a hundred miles west of the Phosphoria ammonoid localities, small silicified representatives of *Perrinites hilli* (Smith) have been found. No detailed information is available in regard to them, but presumably they are Leonardian in age.

*Utah.*—About 150 miles to the south of the Idaho-Wyoming localities, there are contemporaneous ammonoid-bearing strata in the Wasatch Mountains near Provo, Utah. These beds have been identified as the Park City Formation and have been correlated with the Meade Peak member of the Phosphoria. The ammonoids occur abundantly in black shales but are crushed (Pl. 134, fig. 11,12); they appear to be identical with those of the Sublette Range. These specimens are uniformly small and are presumably somewhat dwarfed as are those in the black phosphate rock at the northern locality.

Girty listed *Gastrioceras* sp. together with nautiloids from the Permian Kaibab Limestone of the San Rafael Swell in central Utah (McKee, 1938, p. 165). The exact nature of this ammonoid is not known.

*Nevada.*—Each of the three localities in this state should be regarded as a separate occurrence. The northeasternmost one, in the Montello Range, has yielded only a single specimen, but it is significant as it represents the genus *Properrinites*, *P. nevadensis* M., F., & C., n. sp. The lithology, black shale and thin limestone, is suggestive of the Phosphoria (Cheney et al., 1956, p. 1763–1764). Associated fusulinids have been determined to be upper Wolfcampian. The nearest relatives of *P. nevadensis* occur in the Wichita Group of north-central Texas and the Hueco of westernmost Texas.

From the locality in Carlin Canyon, Nevada, about 100 miles southwest of Montello, we have two small Permian ammonoids: *Crimites elkoensis* M., F., & C., n. sp., and *Daraelities leonardensis* M. & F. The exact stratigraphic relationships of the containing beds are unknown, as there is a thick sequence of Pennsylvanian and Permian conglomerates and limestones. The cephalopods were collected from dense limestone with Wolfcampian fusulinids. The identification of a Leonard ammonoid species, *D. leonardensis*, here is not particularly significant for the genus shows only a single stable evolutionary trend. *Crimites* has not previously been reported in America; similar species occur in both the Sakmarian and Artinskian of the Urals.

A thick Permian limestone section occurs in east-central Nevada near Ely. A search for ammonoids there has yielded only a very few poorly preserved crushed specimens. The only ones that appear to be generically identifiable belong in *Properrinites* and *Crimites*. They are probably conspecific with the forms that occur in northeastern Nevada. Fusulinids are common throughout this general area; those described by Knight (1956) from nearby are Middle Permian, but Thompson (1954, p. 27) reports various Wolfcampian localities in this region. The ammonoids are suggestive of late Lower Permian.

*Arizona.*—In the southeast corner of the state, Permian ammonoids are known from three localities. The eastern two, the Colina and Naco limestones of Cochise County, have yielded only *Perrinites hilli* (Smith), an index species of the Leonardian. The same species has been found at several localities more than 200 miles to the east in New Mexico, Texas, and Chihuahua. At the last of these three, specimens were recently discovered during a Twentieth International Geological Congress Field Trip to Placer de Guadalupe. From another locality, in the Snyder Hill Limestone of the Mustang Mountains in Santa Cruz County, Stoyanow (1949) recorded the discovery of small *Pseudogastrioceras* and *Popanoceras*. His specimens are so immature and poorly preserved that we cannot be certain in regard to their affinities. No ammonoids have been reported from the widespread Kaibab Limestone of northern Arizona,*

* While this report was in press, Mackenzie Gordon, Jr., lent us some specimens of *Pseudogastrioceras* aff. *P. simulator* (Girty) from the Kaibab near Lees Ferry, Coconino County, north-central Arizona. They occur abundantly in brownish-gray banded chert on Soap Creek, about 100 ft. below Highway 89 bridge, a quarter

but Miller & Youngquist (1949, p. 9) record a variety of Permian nautiloids: *Mooreoceras*, *Domatoceras*, *Stearoceras*, *Tainoceras*, *Aulametacoceras*, and *Metacoceras*.

*Sonora.*—Two small silicified specimens of *Waagenoceras dieneri* Böse are known from west of Caborca. G. Arthur Cooper found these in association with a variety of brachiopods and other fossils. The ammonoids occur near the top of a 2000 ft. Permian section in the "*Spiriferellina* zone" of Guadalupian age.

*California.*—From the Bird Spring Formation in the Providence Mountains of southern California, John C. Hazzard secured a few small silicified Permian ammonoids. Unfortunately we can not recognize their affinities. This region has yielded fusulinids of both Lower and Middle Permian age (Thompson et al., 1946, p. 40).

Years ago, T. W. Stanton obtained an ammonoid from the Wildwood Limestone in the southern Klamath Mountains, Trinity County, northern California. No additional collections have since been recorded. J. P. Smith recognized that the affinities of the specimen are with *Stacheoceras*, a genus that ranges throughout the Permian. A sequence of Wolfcampian, Leonardian, and Guadalupian fusulinids is known from this general region, the McCloud and Nosoni formations of the Redding area in Shasta County.

*Oregon.*—A single ammonoid, *Eoasianites merriami* M. & F., has been described from Crook County, central Oregon. It came from a relatively small inlier but was found in "float." The species is not distinctive but is probably Lower Permian.

*British Columbia.*—Permian ammonoids are known from two localities in southwestern Canada. The Cache Creek Series near Kamloops has yielded the following:

*Agathiceras* cf. *A. suessi* Gemmellaro
*Pseudogastrioceras?* sp.
*Adrianites warreni* Miller & Crockford
*Propinacoceras americanum* Miller
*Paraceltites?* sp.

This assemblage was collected by M. B. Crockford over a period of years. It is not diagnostic but is indicative of a Guadalupian age. The fusulinids which occur near the top of this section have been interpreted as being Leonardian or early Guadalupian.

Some 275 miles to the east of Kamloops, near Fernie, Hans Frebold found a single ammonoid in a glacial boulder. The general form, ornamentation, and sutures suggest a relationship to certain of the Lower Permian gastrioceratids recorded from the Urals.

*Summary.*—Permian strata are widespread in the states west of the Rockies. The few ammonoids that have been collected are by no means representative of the sections exposed. Our present understanding of the faunas is based, for the most part, on one or two mediocre specimens from localities a hundred miles or more apart. Whereas ammonoids appear to be rare in this region, it should be recognized that almost invariably they are sporadic, and considerable effort is required to make extensive collections even in the classic areas. An additional search for these fossils in the Basin and Range Province will almost certainly yield results far beyond the scope of this study.

The stratigraphic range of the great majority of Permian ammonoid genera has been established; many are particularly good index fossils. They appear to be reasonably independent of facies and provincialism; none of the forms encountered in this large territory are bizarre. There is little or no reason to differentiate a Tethyan faunal assemblage, and the ammonoids known from America are in general like those of the Mediterranean and southern Asiatic regions.

## SYSTEMATIC PALEONTOLOGY

### PROPERRINITES NEVADENSIS Miller, Furnish & Clark, n. sp.

Pl. 133, fig. 1, 2

We have a single specimen of *Properrinites* from northeasternmost Nevada. It is moderately well preserved in black somewhat silicified limestone. The maximum overall diameter of this fossil measures about 31 mm.; the corresponding width and height of conch are about 19 mm. and 16 mm., respectively; and the umbilicus attains a diameter of some 6½ mm. The

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mile east of Cliff Dweller's Lodge (U. S. Geol. Surv. Loc. 14616 blue [SW¼ sec. 27, T. 39 N., R. 6 E.]; collector, J. P. Akers 1953). The largest attains a diameter of 16 mm. but is completely septate, and it is well preserved in crystalline silica. Its sutures and ornamentation are similar to those of *P. simulator* in the Phosphoria.

whorls are evenly rounded ventrally, and the umbilical borders are moderately distinct.

The surface of the internal mold bears somewhat sinuous transverse constrictions, which form slight ventral sinuses and ventrolateral salients, and which are about a quarter-volution apart. Fragments of the test reveal that it was virtually smooth, though none remains on the umbilical zones of the specimen. The ventral portion of the sutures can be seen on the inner volutions; they are similar to those of *P. vicinus* M. & F. from the Wichita Group of north-central Texas (Miller & Furnish, 1940, p. 142, text-fig. 39B).

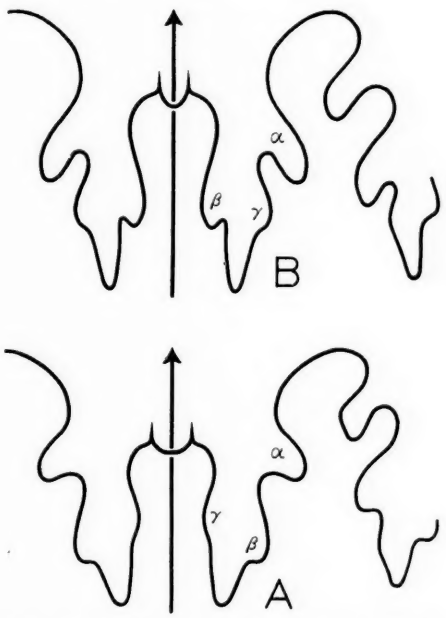
We also have a small crushed perrinitid from east-central Nevada, and it is presumably conspecific. Its greatest overall dimension is 15 mm. (part of which is due to crushing), and its umbilicus is some $4\frac{1}{2}$ mm. in diameter. Portions of the sutures are clearly discernible, and though somewhat distorted, they indicate unmistakably that the individual belongs in *Properrinites*.

*Remarks.*—Insofar as sutures are concerned, this form is more or less intermediate between typical *Properrinites* and *Perrinites*. However, the shape of its conch and the relatively large umbilicus indicate a closer relationship to the former.

Normally there is a fundamental difference in the ontogenetic development of the ventral lobe in *Properrinites* and *Perrinites* (Miller & Furnish, 1940, p. 140):

> In most of the known American representatives of *Properrinites* a digit is developed on the ventral side of the prongs (major subdivisions) of the ventral lobe before the second digit is developed on the dorsal side of those prongs. however, in typical *Perrinites* the reverse is the case; that is, a second digit is developed on the dorsal side of the prongs of the ventral lobe before any digits are developed on the ventral side of those prongs. Nevertheless, this character does not appear to be a reliable means of generic distinction, and the two genera should be differentiated only on the basis of relative complexity of the sutures.

As shown by Text-figure 2B, in typical *Properrinites cumminsi* (White) the sutures display the characteristic features of the genus but are more advanced than the type species, *P. boesei* (Plummer & Scott) of the Admiral Formation in north-central Texas.




TEXT-FIG, *2*—Ventral portions of sutures in *Properrinites*.

A) *P. nevadensis* M., F., & C., n. sp., based on the immature portion of the holotype (State Univ. Iowa, 5999) at a diameter of about 10 mm., from the Wolfcampian of Elko Co., Nevada, ×15.

B) *P. cumminsi* (White), based on a topotype (State Univ. Iowa, 5983) at a diameter of about 15 mm., from the Wichita Group, Baylor Co., Texas, ×8.

*P. nevadensis* (Text-fig. 2A) is quite distinct and has only an incipient digit on the ventral side of the prongs of the ventral lobe. In this respect, it resembles *P vicinus* Miller & Furnish of north-central Texas, which occurs in strata of virtually the same age as those yielding *P. cumminsi*. In *P. vicinus* the umbilicus is larger than that in *P. nevadensis*, but otherwise the proportions of the conch are similar.

*Occurrence.*—The holotype came from the lower Phosphoria equivalent (upper Wolfcampian, *fide* Grant Steele) in dark thin-bedded fusulinid limestone associated with black shale exposed in a nearly vertical sequence in Wild Hoss Canyon, on the east side of Montello (Leach) Range, northeastern Elko County, Nevada (NW $\frac{1}{4}$ sec. 23, T. 41 N., R. 68 E.). There are numerous

large bellerophontids at this locality. Collected by M. B. Stam, H. J. Trepagnier, and W. M. Furnish, 1954.

The crushed specimen referred to this species with question came from the Illapah-Jakes Valley area about 30 miles west of Ely, White Pine County, Nevada. The specimen came from thin-bedded light-brown limestone exposed in low hills west of a side-road 1.6 mi. from junction of road to Hayden Creek well with the Illapah road, some 15 mi. south of Illapah (sec. 27, T. 15 N., R. 59 E.). Collected by David L. Clark, 1956.

*Repository.*—State Univ. Iowa, 5999 (holotype) and 5986 (questionable crushed specimen).

### PERRINITES HILLI (Smith)
Pl. 133, fig. 5, 6

*Perrinites hilli* MILLER, 1944, Geol. Soc. Amer., Spec. Paper. 52, p. 118–119 [synonomy].
PERRINITES sp. WILLIAMS (*fide* Miller), 1954, U. S. Geol. Surv., Prof. Paper 266, p. 38,39,40; ——, 1956, U. S. Geol. Surv., Prof. Paper 281, p. 52.

A fine large silicified individual from southeastern Arizona was loaned to us by Floyd F. Sabins. In size and general physiognomy, it resembles hundreds of specimens from Texas and Coahuila that we have identified as *P. hilli*, and its sutures correspond closely to what we regard as typical of the species in a restricted sense (Miller & Furnish, 1940, p. 148–149). The maximum diameter of this specimen, which is septate throughout, is estimated at 100 mm. The corresponding maximum height and width of conch are both about 50 mm. Umbilical margins are rounded, and the umbilicus is moderately small.

*Remarks.*—The genus *Perrinites* is indicative of Leonardian age but is now known to be represented in the basal portion of the type Word formation in the Glass Mountains, West Texas. It occurs abundantly in Leonardian strata in north-central and western Texas, as well as in southwestern Coahuila; it is the characteristic fossil at many localities. The genus is also known from Central America, northern South America, Timor, Crimea, and Soviet Central Asia. Peculiarly, it does not occur in the well known contemporaneous Artinskian strata of the Ural region. All described forms are remarkably similar.

*Occurrence.*—The illustrated specimen was collected in 1954 from the lower Colina Limestone on a ridge west of the King of Lead Mine (NW ¼sec. 18, T. 16 S., R. 30 E.) in the Chiricahua Mountains of east-central Cochise County, Arizona. Conspecific material from the same formation was identified a few years ago. It came from a locality about 50 mi. to the west in central Cochise County (NE ¼sec. 7, T. 21 S., R. 23 E.)—U.S.G.S. Loc. 8505, James Gilluly, 1937. Also, two small representatives of *P. hilli* are known from a third locality in the eastern Great Basin: south of Roy, southeastern Idaho.

*Repositories.*—Figured specimen, Yale Peabody Museum, 20215. The Arizona specimens from central Cochise County are at the U. S. National Museum. The Idaho material is to be described by Walter Sadlick.

### POANOCERAS? sp.

*Popanoceras bowmani* STOYANOW, 1949, Geol. Soc. Amer., Bull., vol. 60, p. 1946.

This specimen is so small and poorly preserved that its generic affinities are uncertain. The somewhat flattened lateral areas are suggestive of *Popanoceras*. However, we have a full suite of growth stages in *P. bowmani* (Böse) and they are not the same.

*Occurrence.*—Snyder Hill Limestone (upper Leonardian or lower Guadalupian portion) in the Mustang Mountains, northeastern Santa Cruz County, southern Arizona. Found by Donald L. Bryant in association with another small ammonoid, *Pseudogastri oceras*? sp.

*Repository.*—Stoyanow Collection, G2-6100, University of Arizona.

### STACHEOCERAS GORDONI M., F., & C, n. sp.
Pl. 134, fig. 1–4

*Stacheoceras* sp. SMITH, 1903, *in* Diller, Amer. Jour. Sci., ser. 4, vol. 15, p. 350; MILLER & FURNISH, 1940, Geol. Soc. Amer., Spec. Paper 26, p. 22.

Through the courtesy of Mackenzie Gordon we were loaned for study the Klamath (Yallo Bally) Mountain specimen which J. P. Smith recognized as belonging in

*Stacheoceras*. This California individual is well preserved in dark crystalline limestone. The illustrations on the accompanying plate portray only the inner volutions; fragments which adhere to them show that the conch, when complete, formed at least two more whorls and attained a diameter more than twice that of the figured portion.

Exact dimensions have little significance as the specimen is distorted, but the general proportions are clear. The figured part of the specimen is about 22 mm. in diameter, and near its adoral end the conch is about 12 mm. wide. The umbilicus is small but not closed.

Fragments of the test show that the surface bears fine growth lines. Presumably these are parallel to prominent constrictions on the internal mold, and they are almost straight and directly transverse but form slight lateral salients.

The sutures (Text-fig. 3) show clearly.

TEXT-FIG. 3—External suture of *Stacheoceras gordoni* M., F., & C., n. sp., based on the holotype (U. S. Nat. Mus., 119749) at a diameter of 23 mm., from the Wildwood Limestone of Trinity County, California, ×4.

Each external one forms a prominently bifid ventral lobe and, on either side of it, nine lateral and auxiliary lobes as well as an umbilical lobe. The prongs of the ventral lobe are bifid. The first lateral lobe is primarily bifid but secondarily quadrifid. The remaining lateral and auxiliary lobes are more or less trifid, except for the one on the umbilical margin, which is bifid. The relatively broad umbilical lobe is subdivided. A septum shows that the internal lateral and auxiliary lobes are equal in number to those of the external suture and are paired with them; only portions of their details can be observed on fragments of the test. However, it can be seen that the dorsal lobe is prominently trifid, as in the type species of the genus.

*Remarks*.—Though this species is clearly referable to *Stacheoceras*, its conch is narrow for the genus. Also, the sutures are of an advanced type. None of the forms known from America are closely similar. The sutures of *S. gaudryi* Gemmellaro of the Sicilian Middle Permian have the same number of lobes, but the conch of that species is much thicker. *S. antiquum* (Waagen) of the Upper Permian in the Salt Range and the Himalayas also has comparable sutures but a wider conch. *S. tschernyschewi* (Stoyanow) of the Upper Permian in Armenia is another form that has comparable sutures, but the only illustrated representative of it appears to have been crushed. Of the many types of *Stacheoceras* known from the Permian of Timor, the closest are perhaps those described by Haniel as *Popanoceras tridens* forms $\epsilon$ and $\zeta$. Collectively, these specific comparisons suggest that *S. gordoni* is Middle or Upper Permian in age. A sequence of Permian fusulinid faunas has been described from the McCloud Limestone about 50 mi. to the northeast of the locality which yielded our holotype; however, the relationship of the fusulinid and ammonoid beds is not known.

*Occurrence*.—This ammonoid was collected by T. W. Stanton in 1902, who noted that it came from near the top of a 200-foot limestone unit dipping steeply to the southwest and forming a prominent ridge. Associated fossils included crinoids, corals, brachiopods, and another ammonoid. The locality (U.S.G.S. loc. 3977, green) is near the Hall City mines (sec. 32, T. 30 N., R. 10 W.) about 3 mi. northeast of Wildwood, Trinity County, northern California.

*Holotype*.—U. S. National Museum, 119794.

### PSEUDOGASTRIOCERAS spp.
Pl. 134, fig. 8–12

*Paragastrioceras* sp. BISSELL, 1952, Amer. Assoc. Petrol. Geol., Bull., vol. 36, p. 591.

Permian black shales in the southern Wasatch contain an abundance of ammonoids preserved as flattened molds. All of these appear to be of the same general type and probably are referable to *Pseudogastrioceras*. Most attain only moderate size (20 to 30 mm. in diameter), all have prominent spiral sculpture, and a few retain faint traces of portions of the sutures. Umbilical nodes and ribs are discernible on some,

whereas others are transversely marked only by constrictions and fine growth-lines. All the determinable specific characters of these specimens are reminiscent of the gastrioceratids which characterize the phosphate beds of the Phosphoria Formation near the Wyoming-Idaho boundary. As shown by the illustrations on the accompanying plate, these specimens reveal a considerable amount of variation and are probably referable to more than one species.

*Occurrence.*—The dark phosphatic shale member of the Park City Formation (=Meade Peak Member of Phosphoria Formation), probably Leonardian in age. The ammonoids are found in black calcareous "slabby" shale associated with numerous small bellerophontids. The locality is in the Right Fork of Hobble Creek Canyon, southeast of Provo, Wasatch County, Utah. Collected by Walter Youngquist, 1949, and David L. Clark, 1956.

*Figured specimens.*—State Univ. Iowa, 5987 and 5988.

PSEUDOGASTRIOCERAS? sp.

*Paragastrioceras serratum* STOYANOW, 1949, Geol. Soc. Amer., Bull., vol. 60, p. 1946.

Through the courtesy of Donald L. Bryant, we were loaned the small specimen which Stoyanow had identified with a Guadalupe species. Like the holotype of *Gastrioceras? serratum* Girty, this individual is small and immature. Presumably both would have assumed the characteristics of *Pseudogastrioceras* at maturity. However, in few cases are the inner volutions of the many large West Texas gastrioceratids similar to these small specimens.

*Occurrence.*—Snyder Hill Limestone (upper Leonardian or lower Guadalupian portion) in the Mustang Mountains, northeastern Santa Cruz County, southern Arizona. Found in association with another immature silicified ammonoid, *Popanoceras?* sp. Collected by Donald L. Bryant.

*Repository.*—Stoyanow Collection, G2-6106, University of Arizona.

Genus SPIROLEGOCERAS M., F., & C., n. gen.
Type species: *S. fischeri* M., F., & C., n. sp.

This genus is established for subdiscoidal metalegoceratids with prominent longitudinal sculpture and sutures in which the prongs of the ventral lobe are relatively large. As in other members of the family, the sutures form a total of 12 lobes of which the external and the internal second laterals are developed on the flanks of the umbilical lobe.

The type species is from the mid-portion of the Permian Phosphoria formation in the central Rocky Mountain region. A large congeneric form is known from beds, presumably of the same general age, in Arctic America. As a matter of expediency, we are regarding *Spirolegoceras* as an independent genus rather than a subgenus of *Metalegoceras.*

SPIROLEGOCERAS FISCHERI M., F., & C., n. sp.
Pl. 134, fig. 5–7

A small collection of Phosphoria goniatites was secured by Alfred G. Fischer, and it contains two specimens which belong in an undescribed species, the type of the new genus *Spirolegoceras.* The better of these, which is illustrated, is designated the holotype.

Both individuals are internal molds to which large portions of the test adhere, and they represent the phragmocone and the adapical half-volution of the body chamber. The maximum overall diameter of each specimen measures some 20 mm. At the junction of the phragmocone and the body chamber, the conch is about 13 mm. in diameter; its height and corresponding width are about 7 mm., and 8 mm., respectively; and the umbilical dimension is about 3 mm. In shape the conch is thickly subdiscoidal, with an evenly rounded venter.

The test is reticulate, with the longitudinal lirae being much the stronger. Both type specimens bear sinuous transverse constrictions which are more pronounced

TEXT-FIG. 4—*Spirolegoceras fischeri* M., F., & C., n. gen., n. sp., based on the holotype (State Univ. Iowa, 5997) at a diameter of 10 mm., from the Phosphoria Formation just east of Montpelier, Idaho, ×6.

on the internal mold than on the exterior of the test, which are characterized by closely crowded growth lamellae, and which are almost directly transverse but form shallow lateral sinuses and ventral salients.

The suture consists of a broad bifid ventral lobe and on either side of it an inverted-U-shaped first lateral saddle, and attenuated first lateral lobe, a second lateral saddle similar to the first but smaller, a small asymmetric second lateral lobe, a low broad saddle at the umbilical shoulder, and a small somewhat V-shaped lobe on the umbilical wall. The internal suture is visible on a septum of the paratype; it consists of a dorsal lobe and on either side of it two lateral lobes of which the one near the umbilical seam is relatively small. The lateral lobes, both external and internal, adjacent to the umbilicus are formed adventitiously as subdivisions of the umbilical lobe. The first lateral lobe of the external suture is of somewhat the same size as the prongs of the ventral lobe and, like them, is very narrowly rounded, but it is much more attenuated. The secondary saddle in the ventral lobe is about three-fourths as high as the lobe is deep, and its flanks are subparallel.

*Remarks.*—This species is quite distinct in several ways from all described forms. The goniatites known from the Phosphoria Formation are much smaller than is normal for the genera in which they belong, and the Arctic species related to *S. fischeri* is large.

One of the more diagnostic features of the form under consideration is the relatively large ventral lobe of its sutures. Each prong of that lobe has approximately the same area as the first lateral lobe; in the type species of *Metalegoceras* the area of a ventral prong is only about 60 percent as great. In certain other Goniatitaceae comparable differences in the sutures are regarded as of fundamental significance.

The strong spiral sculpture of *S. fischeri* is also distinctive. However, in certain species of *Metalegoceras* faint lirae are present on the umbilical portions of the test.

Furthermore, it should be mentioned that in most other metalegoceratids the whorls are relatively broad, particularly in specimens of a comparable size. The conch proportions in *S. fischeri* represent an extreme for the family.

*Occurrence.*—Concretions in black shale some 10–15 feet above a limestone which directly overlies main phosphate beds in the Meade Peak Member of the Phosphoria Formation at the "old mine" just east of Montpelier, Idaho.

*Repository.*—State Univ. Iowa, 5996 (paratype) and 5997 (holotype).

### Genus CRIMITES Toumansky

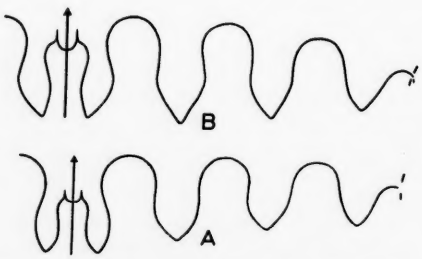
Type species: *C. pamiricus* Toumansky

This genus includes forms with globular conchs, small umbilici, crenulate or reticulate surface sculpture, and external sutures that consist of a bifid ventral lobe and three pointed lateral lobes. The umbilical portions of the suture may be erratic and differ on opposite sides of the same specimen. The internal suture consists of lobes paired with those of the external; a complete suture forms 14 lobes plus small inflections on the umbilical wall. Representatives of the genus are known from beds of Sakmarian and/or Artinskian age in the Urals, Crimea, Pamirs, Timor, and Nevada.

The adrianitids, which include this genus, are common and diversified in the classic Permian of Sicily, the Urals, and Timor. However, in America they are relatively rare. A few primitive forms are known from Pennsylvanian strata in this continent, and a moderate representation of the group is found in the Permian. The unique genus *Texoceras* of the West Texas Leonardian is a close relative of *Crimites* but differs in the shape of the conch and the details of the sutures.

#### CRIMITES ELKOENSIS M., F., & C., n. sp.

This species is based on a single fragment which represents a portion of a phragmocone. The conch is globular in shape, being considerably wider than high and broadly rounded ventrally. It is estimated that the maximum diameter of the preserved part of this holotype was some 8 mm., and that the corresponding width of conch was about 10 mm. The umbilicus is small but not closed. No portion of the test is preserved. Each suture (Text-fig. 5) forms a bifid ventral lobe and on either side of it three pointed linguloid lobes. The umbilical por-




TEXT-FIG. 5—External sutures of *Crimites*.
A) *C. elkoensis* M., F., & C., n. sp., based on the holotype (State Univ. Iowa, 5984) at a diameter of about 8 mm., from the Wolfcampian of Elko County, Nevada, ×7.
B) *C. krotowi* (Karpinsky), based on a specimen (State Univ. Iowa, 5981) at a diameter of 15 mm., from the Artinskian of the Southern Ural region, ×4.

tion of the suture is not retained, but presumably there was one or more small lobes on the umbilical wall.

We are doubtfully referring to this species a specimen from a locality some 125 mi. to the south of that which yielded the holotype. It is a crushed individual upon which several sutures are clearly visible; these have the shape that is characteristic of the genus. Also, a possible trace of reticulate surface markings can be discerned. In its present crushed state, this specimen has a diameter of some 20 mm. and an umbilicus about 2 mm. in width.

*Remarks.*—The material upon which we base our understanding of this species is only moderately satisfactory. However, these two specimens are clearly referable to *Crimites*, and they are the first representatives of the genus to be reported from America. Because of their incompleteness and rather poor preservation, it is not possible to make detailed comparisons with congeneric forms known from Eurasia.

*Occurrence.*—The holotype came from light-brown dense limestone of middle Wolfcampian age in North Carlin Canyon (sec. 10, T. 33 N., R. 53 E.), some 20 mi. west of Elko, Elko County, Nevada. It was secured in 1955 by Curtis Little, and Grant Steele determined the age of associated fusulinids. The specimen referred to this species with question is on a slab of brown to yellow limestone from low hills west of a side-road 1.6 mi. from junction of road to Hayden Creek well with Illapah road (sec. 27, T. 15 N., R. 59 E.), White Pine County, Nevada. This specimen, together with a few other poorly preserved ammonoids, was collected by David L. Clark in 1955.

*Repository.*—State Univ. Iowa, 5984 (holotype) and 5985 (questionable representative of species).

### DARAELITES LEONARDENSIS Miller & Furnish

*Daraelites leonardensis* MILLER & FURNISH, 1940, Geol. Soc. Amer., Spec. Paper. 26, p. 13,20,63, 64,65, pl. 33, fig. 6,7; RUZHENCEV, 1950, Akad. Nauk SSSR, Trudy Paleont. Inst., t. 29, p. 53; ——, 1956, ibid., t. 60, p. 79,82.

Grant Steele sent us a small block of Permian limestone from Nevada that contained a representative of this species and one of the adrianitid genus *Crimites*. The daraelitid is incomplete and only moderately well preserved, but it reveals the significant characters. It is septate throughout and appears to represent the adoral portion of a mature phragmocone. Its overall diameter is about 20 mm., and near its adoral end the height and corresponding width of conch are some 10 mm. and 6½ mm., respectively. Presumably, the conch, when

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### EXPLANATION OF PLATE 133

FIG. *1,2*—*Properrinites nevadensis* M., F., & C., n. sp. The holotype, from Wolfcampian limestone in Wild Hoss Canyon, Montello Range, northeastern Elko County, Nevada, ×2; State Univ. Iowa, 5999.

*3–6*—*Perrinites hilli* (Smith). *3,4*, A specimen from the lower portion of the Word Formation (First Limestone Member) in the Glass Mountains, Brewster County, Texas, ×1½; Amer. Mus. Nat. Hist., 28023. *5,6*, A specimen from the lower Colina Limestone in the Chiricahua Mountains, Cochise County, Arizona, ×1; Yale Peabody Mus., 20215.

*7,8*—*Stacheoceras normani* M. & F., n. sp. The holotype from the lower portion of the Word Formation (First Limestone Member) in the Glass Mountains, Brewster County, Texas, ×1½; Amer. Mus. Nat. Hist., 28022.

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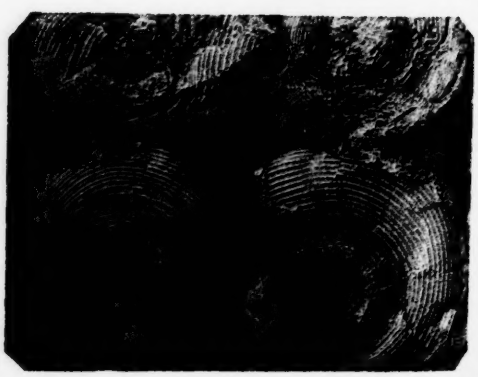
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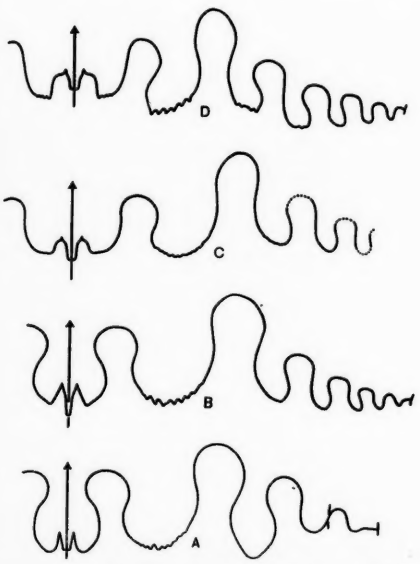


TEXT-FIG. 6—Mature sutures of Daraelitidae, showing a phylogenetic sequence.

A) *Epicanites culmiensis* (Kobold)?, based on a specimen (State Univ. Iowa, 5995) from the upper Viséan of County Leitrim, Eire, at a diameter of 20 mm., ×6.

B) *Boesites texanus* (Böse), based on a topotype (Yale Peabody Mus., 16777) from the Gaptank Formation of West Texas, at a diameter of 14 mm., ×7.

C) *Daraelites* cf. *D. leonardensis* Miller & Furnish, based on a specimen (State Univ. Iowa, 5998) from the Wolfcampian in Carlin Canyon, Elko County, Nevada, at a diameter of 18 mm., ×5.

D) *Daraelites meeki* Gemmellaro, based on a specimen (Yale Peabody Mus., 15214) from the Sosio Limestone, province of Palermo, Sicily, at a diameter of 25 mm., ×4.

complete, was about another half-volution in length. The umbilicus is moderate in size, and the umbilical shoulders are indefinite.

Near the adoral end of this specimen, the external sutures form a broad trifid ventral lobe and on either side of it a rounded linguliform saddle, a moderately large asymmetrical first lateral lobe, a high rounded second lateral saddle, and a series of relatively small rounded lobes and saddles which decrease in size toward the umbilicus. At least the lateral prongs of the ventral lobe, and the first lateral lobe, are finely serrate, but the details are obscure.

*Remarks.*—Both the holotype and the paratype of this species are rather poorly preserved, but they reveal the diagnostic characters. All members of the family are closely similar, and they represent a single evolutionary sequence. The form under consideration is distinctly intermediate between *Boesites kingi* (Plummer & Scott) of the early Wolfcampian and *Daraelites meeki* Gemmellaro of Guadalupian age.

*Occurrence.*—The specimen is preserved in dense light-brown limestone with small scattered bluish-white coloform siliceous structures. It was found in association with middle Wolfcampian fusulinids (*fide* Grant Steele), as well as *Crimites elkoensis*. The locality is North Carlin Canyon (sec. 10, T. 33 N., R 53 E.), some 20 miles west of Elko, Elko County, Nevada. The species was originally described from the middle Leonard of the Glass Mountains, West Texas, the only place from which it has been reported previously.

*Repository.*—State Univ. Iowa, 5998.

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EXPLANATION OF PLATE 134

FIG. *1–4*—*Stacheoceras gordoni* M., F., & C., n. sp. The holotype (U. S. Nat. Mus., 119749) from the Wildwood Formation near Wildwood Ranch, Trinity County, California, ×2½.

*5–7*—*Spirolegoceras fischeri* M., F., & C., n. gen., n. sp. The holotype (State Univ. Iowa, 5997) from the Meade Peak Member of the Phosphoria Formation east of Montpelier, Idaho, ×3.

*8–12*—*Pseudogastrioceras* spp. *8,9*, Two views of a specimen (State Univ. Iowa, 5989) from the Meade Peak Member of the Phosphoria Formation, Raymond Canyon, Sublette Range, westernmost Wyoming, ×2½. *10*, Another individual (State Univ. Iowa, 711) from the same general horizon and locality as the preceding, ×2½. *11,12*, Two slabs (State Univ. Iowa, 5988 and 5987) from the lower Park City Formation, Hobble Creek Canyon, Wasatch Mountains, southeast of Provo, Utah, ×2 and ×3.

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JOURNAL OF PALEONTOLOGY, VOL. 31, NO. 6, P. 1069–1108, PL. 135–142, 8 TEXT-FIG., NOVEMBER 1957

# EARLY UPPER DEVONIAN (INDEPENDENCE) CONODONTS FROM IOWA, PART I

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ABSTRACT—Conodonts are suitable for detailed zonation within the Upper Devonian. No complete section of this time interval is yet known in North America with a lithology favorable for processing. Correlation, therefore, has to rely upon a composite sequence of conodont faunas, the relative ages of which have been established by other index fossils. In Iowa, excellently preserved and rich assemblages of the higher portion of early Upper Devonian are described from the Amana, Independence, Sweetland Creek, and North Liberty beds, as well as from a sinkhole in the Cedar Valley limestone at Solon. These sequences occur in a transgressive sediment upon Middle Devonian Cedar Valley limestone and are all considered as belonging to the Independence formation. Differences in composition of the macrofauna in some of those beds are recognized as due to environmental reasons. The conodonts are apparently little affected by bottom conditions and reveal more detailed subdivisions, particularly in the Amana sequence. The North Liberty beds include the oldest parts of the formation and belong to the middle zone of early Upper Devonian. The microfauna, other than conodonts, is mainly megaspores, hystrichosphaerids, foraminifers, scolecodonts, holothurian spiculae, ostracodes, and fish remains.

In the systematic portion, 9 conodont genera with 34 species are described. Newly established are 8 species, 2 genera (*Ctenopolygnathus*, type: *Polygnathus angustidisca* Youngquist, 1945, range: Devonian-Mississippian; and *Ancyropenta*, type: *Ancyrognathus curvata* Branson & Mehl, 1934, range: early Upper Devonian), and 1 family (Icriodidae).

## INTRODUCTION

STUDIES of the European sections indicate conodont species have excellent time sensitivity and can be used for zonation within the Upper Devonian. They are so widely distributed in many limestones and shales, that conodonts can be regarded as ideal index fossils of this time. However, too little is known of the morphology of species as well as geologic ranges. A better understanding of the species can be attained by intensive, comparative study of material from continous and fossiliferous sections. However, in order to recognize admixtures it may be necessary to investigate several distant localities and, on the basis of abundant material, trace evolutionary trends within single partial-genera or even within the species.

Unfortunately, the localities for previous studies in North America expose only one or, at most, a few conodont-bearing horizons Also, these localities are too far apart to be correlated exactly by physical stratigraphic means. Therefore, few authors have been in a position to realize fully the possibilities for a subdivision of the Upper Devonian on the basis of conodonts. An exception, the Grassy Creek fauna of Branson & Mehl (1934), includes species equivalent to several zones in the Frasnian and Famennian in Europe. If the collections do not contain stratigraphic admixtures, it should be possible to subdivide these sediments into at least three or four zones.

Since the original investigations of Branson & Mehl, some progress has been made in subdivision of the Upper Devonian of North America. Hass (1951) was able to demonstrate three zones within the middle division of the Arkansas Novaculite at Caddo Gap, Montgomery County, Arkansas. The lowest fauna is regarded as a time equivalent of the fauna in the present report. The second association is an equivalent of the Famennian in Europe, and the youngest is early Kinderhookian (Lower Mississippian). Unfortunately it was not possible to disintegrate shales of the type present at Caddo Gap and to isolate the conodonts from the matrix. Therefore, Hass had to rely on rubber replicas which could be secured only from one side and which are more difficult to study than the

isolated conodonts. His figures and determinations cover only a fraction of the representation in the zones. These data are adequate for age determination of the beds in his study, but any application of the findings elsewhere is difficult; particularly so, if the fauna to be compared is also only a partial representation and is poorly preserved.

In the Upper Devonian of North America no continous sections are known to contain abundant conodonts which can be readily secured. Such a section may be present somewhere in the Rocky Mountains, where little conodont work has yet been done. Meanwhile, another way to define conodont zones within the American Upper Devonian has to be attempted—a comprehensive study of representative faunas from individual zones where they are well preserved and abundant. Evaluation of the associated fossils of other groups may link these isolated representations to an idealized standard section.

The conodont faunas of the Amana, Independence, and Sweetland Creek beds are excellent suites for the establishment of a standard. The containing sediments were deposited in a comparatively short time interval during a transgression over the Middle Devonian Cedar Valley limestone. Fortunately, conodonts of the Cedar Valley are so distinct from those described in the present report that the occurrence of an admixture would be relatively easy to recognize. Also, this Upper Devonian fauna is well preserved and abundant, and has a large variety of species. The common occurrence of large specimens seems to indicate that the depositional environment was favorable to the conodont animal.

The macrofauna of the Independence and associated beds is so well known (Miller, 1938; Stainbrook, 1945) that a good correlation can be attained. The beds contain representatives of the goniatite genera *Manticoceras* and *Ponticeras*, which are characteristic for the middle-upper portion of the *Manticoceras*-Stufe in Europe (I beta-gamma, and delta). Many similar or even identical conodont species are common to the beds under consideration and the upper portion of the *Manticoceras*-Stufe in Europe. On the basis of brachiopods "the Independence fauna is the one assemblage in North America most closely related to the '*Cuboides*' zone of Europe as seen in the Frasnian F2 of Belgium" (Coooper & Warthin *in* Cooper et al., 1942; Stainbrook, 1945).

Another rich and well preserved conodont fauna was secured from the Squaw Bay limestone in Michigan with *Koenenites cooperi* Miller, 1938. *Koenenites* in Europe is an index of the lower portion of the *Manticoceras*-Stufe (I alpha). The Squaw Bay species of the diagnostic conodont genera are clearly different from those of the Amana, Independence, and associated beds. Therefore, it may be concluded that in North America, also, subdivisions of the early Upper Devonian may be recognized on the basis of conodont zones.

A comprehensive study of abundant, well preserved and unmixed Famennian associations can next be sought from such units as the New Albany Shale in Indiana, or the Three Forks Formation in Montana. These beds should provide assemblages which are distinct from the earlier Upper Devonian ones, and at least partly from each other. The Kinderhookian (Lower Mississippian) yields conodonts which can be readily distinguished from the Devonian ones.

Conodont species used for zonation can be identified by gross features alone. Therefore, after comprehensive studies of several "guide horizons" are completed, the possibility of correlation on the basis of even fragmentary or only fairly well preserved collections, *e.g.*, from well cuttings, may be expected.

However, some attention must be given to the possibility of environmental differences between assemblages. At the present time, little is known about the occurrence of genera and species in relation to facies. Therefore, it seems to be essential to draw conclusions for correlations only on the basis of the represented species and genera. Negative evidence, such as absence of conspicuous forms abundant elsewhere in the associations, can not be regarded as sufficient to indicate a difference in age.

In our opinion, changes within a genus or even a species following an established evolutionary trend are more valuable for correlation purposes than the presence of con-

spicuous forms belonging to different partial-genera.

### ACKNOWLEDGMENTS

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### DEPOSITION OF TYPES

The figured specimens are deposited in the repository of the State University of Iowa (SUI).

## DESCRIPTION OF BEDS AND LOCALITIES

### AMANA BEDS

Between the Middle and High Amana communities in Iowa County, there is an exposure of gray shales with some interbedded impure limestones. Stainbrook (1945, p. 8) has tentatively termed these sequences "Amana beds" and has regarded the macrofossils to be intermediate between Independence and Lime Creek. According to that author the Amana beds are the Iowa correlative of the High Point (Nunda) of New York.

TEXT-FIG. *1*—Index map of eastern Iowa.

Conodonts were secured from these beds as early as 1936 by W. M. Furnish (unpublished oral communication). Youngquist (1945) has given an account of this fauna, which he correlated approximately with the Olentangy shale of central Ohio. His material was secured from a shale bed within the lower part of the section described here in detail.

The best outcrop is near the village of Middle Amana along State Highway 220, N½ sec. 29, T81N, R9W. The road ditch was enlarged during the summer and fall of 1955, so that the sequence was well exposed for about 1 mile. The beds show a somewhat variable dip which is probably a result of glacial shove. The overlying till is similar in general appearance to the Devonian shales, but is distinguishable by its sand content.

The samples were collected rather by lithologic units than by regular intervals. Beds which seemed to be favorable for the preservation of good conodonts have been exploited more extensively than the remainder. In order to get an abundant fauna, the best layers have been resampled several times. The section is locally distorted and thicknesses of the shales are only approximate. All samples have been collected from

the easternmost 300 yards of the exposure, where the sequence is as follows:

Overlying: gray, arenaceous till.

4′ (bed 13) dark gray, noncalcareous shale with casts of brachiopods and *Ancyrodella buckeyensis* Stauffer, 1938; *A. gigas* Youngquist, 1947; *Ancyropenta longidenticulata*, n. sp.; *Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer, 1938); *P.* (*M.*) *subrecta* (Miller & Youngquist, 1947); *Polygnathus normalis* Miller & Youngquist, 1947?; *P. foliata* Bryant, 1921.

1′ (bed 12) greenish gray shale with *Ancyrodella hamata* Ulrich & Bassler, 1926; *A. gigas* Youngquist, 1947; *Ancyroides princeps* Miller & Youngquist, 1947; *Ancyropenta longidenticulata*, n. sp.; *Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer, 1938); *P.* (*M.*) *hassi*, n. sp.; *P.* (*M.*) *subrecta* (Miller & Youngquist, 1947); *Polygnathus foliata* Bryant, 1921.

Covered interval of a few feet.

2′ (bed 11) gray, noncalcareous shale with *Ancyrodella buckeyensis* Stauffer, 1938; *A. gigas* Youngquist, 1947; *Ancyrognathus amana*, n. sp.; *Ancyroides calvini* Miller & Youngquist, 1947; *A. asymmetrica* (Ulrich & Bassler, 1926); *A. uddeni* Miller & Youngquist, 1947; *Ancyropenta longidenticulata*, n. sp.; *Ctenognathus gradata* (Youngquist, 1945); *Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer, 1938); *P.* (*M.*) *subrecta* (Miller & Youngquist, 1947); *Polygnathus amana*, n. sp.; *P. foliata* Bryant, 1921.

9′ (bed 10) grayish-olive shale with *Ancyrodella buckeyensis* Stauffer, 1938?; *A. hamata* Ulrich & Bassler, 1926; *A. gigas* Youngquist, 1947; *Ancyroides asymmetrica* (Ulrich & Bassler, 1926); *A. princeps* Miller & Youngquist, 1947?; *Ancyropenta longidenticulata*, n. sp.; *Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer, 1938); *P.* (*M.*) *hassi*, n. sp.?; *P.* (*M.*) *subrecta* (Miller & Youngquist, 1947); *P.* (*M.*) *unicornis* (Miller & Youngquist, 1947); *Polygnathus amana* n. sp.; *P. normalis* Miller & Youngquist, 1947; *P. foliata* Bryant, 1921.

5′ (bed 9) grayish-olive shale with *Ancyrodella hamata* Ulrich & Bassler, 1926; *Ctenopolygnathus angustidisca* (Youngquist, 1945); *Palmatolepis* (*Manticolepis*) *hassi*, n. sp.; *P.* (*M.*) *subrecta* (Miller & Youngquist, 1947)?; *Polygnathus amana*, n. sp.; *P. normalis* Miller & Youngquist, 1947; *P. foliata* Bryant, 1921; *P. independensis*, n. sp.

3′ brown, fine-crystalline, dolomitic limestone, conodont fragments only.

4′ (bed 8) grayish-olive shale with *Ancyrodella buckeyensis* Stauffer, 1938; *A. hamata* Ulrich & Bassler, 1926; *Ancyrognathus alta*, n. sp.; *A. amana*, n. sp.; *A. triangularis* Youngquist, 1945; *Ancyroides euglypheus* (Stauffer, 1938); *A. princeps* Miller & Youngquist, 1947; *Ancyropenta asteroideus* (Stauffer, 1938); *A. longidenticulata*, n. sp.; *Ctenognathus gradata* (Youngquist, 1945); *Icriodus symmetricus* Branson & Mehl, 1934; *Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer, 1938); *P.* (*M.*) *foliacea* (Youngquist, 1945); *P.* (*M.*) *hassi*, n. sp.; *Polygnathus normalis* Miller & Youngquist, 1947; *P. foliata* Bryant, 1921; *P. granulosa* Branson & Mehl, 1934; *P. unicornis*, n. sp.

4″ (bed 7) gray, marly, dense limestone (containing the best preserved conodonts) with *Ancyrodella buckeyensis* Stauffer, 1938; *A. hamata* Ulrich & Bassler, 1926; *A. subrotunda* Miller & Youngquist, 1947; *Ancyrognathus amana*, n. sp.; *A. iowaensis* Youngquist, 1947; *A. triangularis* Youngquist, 1945; *Ancyropenta longidenticulata*, n. sp.; *Ctenognathus gradata* (Youngquist, 1945); *Icriodus symmetricus* Branson & Mehl, 1934; *Palmatolepis* (*Manticolepis*) *amana*, n. sp.; *P.* (*M.*) *flabelliformis* (Stauffer, 1938); *P.* (*M.*) *foliacea* (Youngquist, 1945); *P.* (*M.*) *hassi*, n. sp.; *Polygnathus foliata* Bryant, 1921; *P. granulosa* Branson & Mehl, 1934; *P. unicornis*, n. sp.

1′ (bed 6) grayish-olive shale with *Ancyrodella hamata* Ulrich & Bassler, 1926; *Ancyrognathus triangularis* Youngquist, 1945; *Ctenognathus gradata* (Youngquist, 1945); *Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer, 1938); *P.* (*M.*) *foliacea* (Youngquist, 1945); *P.* (*M.*) *hassi*, n. sp.; *P.* (*M.*) *unicornis* (Miller & Youngquist, 1947); *Polygnathus foliata* Bryant, 1921; *P. granulosa* Branson & Mehl, 1934; *P. unicornis*, n. sp.

Covered interval of a few feet.

3′ (bed 5) grayish-olive shale with *Ancyrodella hamata* Ulrich & Bassler, 1926; *Ancyrognathus triangularis* Youngquist, 1945; *Ctenopolygnathus angustidisca* (Youngquist, 1945); *Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer, 1938)?; *P.* (*M.*) *foliacea* (Youngquist, 1945); *P.* (*M.*) *hassi*, n. sp.; *Polygnathus amana*, n. sp.; *P. foliata* Bryant, 1921; *P. granulosa* Branson & Mehl, 1934; *P. unicornis*, n. sp.

Interbedded with marly limestone layers (bed 4) with *Ctenognathus gradata* (Youngquist, 1945); *Palmatolepis* (*Manticolepis*) *foliacea* (Youngquist, 1945); *P.* (*M.*) *hassi*, n. sp.

3′ (bed 3) grayish-olive, calcareous shale with abundant brachiopods, crinoids, and with *Ancyrodella hamata* Ulrich & Bassler, 1926; *A. subrotunda* Miller & Youngquist, 1947; *Ctenognathus gradata* (Youngquist, 1945); *Ctenopolygnathus angustidisca* (Youngquist, 1945); *Icriodus symmetricus* Branson & Mehl, 1934; *Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer, 1938); *P.* (*M.*) *foliacea* (Youngquist, 1945); *P.* (*M.*) *hassi*, n. sp.; *Polygnathus foliata* Bryant, 1921; *P. unicornis*, n. sp.

2′–3′ (bed 2) grayish-olive shale with *Ancyrodella hamata* Ulrich & Bassler, 1926; *Ancyrognathus triangularis* Youngquist, 1945; *Ancyropenta longidenticulata*, n. sp.; *Icriodus symmetricus* Branson & Mehl, 1934; *Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer, 1938); *P.* (*M.*) *foliacea* (Youngquist, 1945);

*P.* (*M.*) *hassi*, n. sp.; *Polygnathus foliata* Bryant, 1921; *P. granulosa* Branson & Mehl, 1934; *P. unicornis*, n. sp.

1′ (bed 1) grayish-olive shale with flat, irregular lenses of marly limestone. Lowermost exposed; limestone with *Ancyrodella hamata* Ulrich & Bassler, 1926; *Ancyrognathus triangularis* Youngquist, 1945; *Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer, 1938); *P.* (*M.*) *foliacea* (Youngquist, 1945); *P.* (*M.*) *hassi*, n. sp.; *P.* (*M.*) *unicornis* (Miller & Youngquist, 1947); *Polygnathus foliata* Bryant, 1921; *P. unicornis*, n. sp.

The total exposed thickness of the Amana beds is about 40 feet. The location is SW¼, NE¼, Sec. 29, T81N, R9W.

The westernmost portion exposed in this road-cut is near an abandoned quarry in a coarse, reddish sandstone of Pennsylvanian age which contains numerous silicified corals, reworked from the Cedar Valley limestone.

5′ (bed W) dark, fine-grained, noncalcareous shale is uncovered in the ditch. The abundant conodont fauna consists of the following species: *Ancyrodella hamata* Ulrich & Bassler, 1926; *A. subrotunda* Miller & Youngquist, 1947?; *Ancyrognathus triangularis* Youngquist, 1945; *Ancyroides uddeni* Miller & Youngquist, 1947; *Ancyropenta longidenticulata*, n. sp.; *Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer, 1938); *P.* (*M.*) *hassi*, n. sp.; *Polygnathus amana*, n. sp.; *P. normalis* Miller & Youngquist, 1947; *P. foliata* Bryant, 1921; *P. unicornis*, n. sp.

Because of insufficient exposure it is impossible to link this sample stratigraphically with the sequence given earlier, but the presence of *Ancyroides uddeni* Miller & Youngquist, 1947, and the lack of lime content in the shale suggest that it correlates with the higher portion of the described sequence.

The late M. A. Stainbrook has given us a shale and limestone sample from an outcrop ½ mile east of the village of High Amana. The conodont fauna is essentially identical with the one of the described section. However, nearly all specimens are fragmentary, and this fauna is therefore not included in the comparison.

### INDEPENDENCE BEDS

The Independence shale was named by Calvin (1878, p. 725) for some argillaceous, fine-grained, bituminous shales near Independence, Iowa, which had been found underneath the Cedar Valley limestone. Stainbrook has guided us to the type locality, a mile east of Independence, Iowa. The debris, thrown out of the pit, is much weathered during the 80 years since the discovery of this shale, and the collected samples produced neither conodonts nor any other of the characteristic marine fossils. However, Stainbrook (1945, p. 1) has confirmed that this locality has yielded megafossils which are identical with those from the outcrops at the nearby county farm. On such evidence, both localities may be presumed to be in the same sediments.

The conodont content of the Cedar Valley limestone appears to be considerably older than the Independence shale. Therefore, the occurrence of the shale underneath the limestone at the type locality is probably due to sedimentation in a sinkhole within the Cedar Valley, as it has been observed at several other localities (Cooper et al., 1942, p 1766).

Conodonts from the Independence shale have been noted by Cushman & Stainbrook (1943, p. 74) and by Stainbrook (1945, p. 2), but are yet undescribed. Our material has been secured at the following localities:

1. From several calcareous shale beds which are interbedded with thin limestone layers in an outcrop on both sides of the road at the county farm near Independence, Buchanan County, Iowa, center Sec. 25, T89N, R9W. Content: *Ancyrodella buckeyensis* Stauffer, 1938; *A. hamata* Ulrich & Bassler, 1926; *Ancyrognathus triangularis* Youngquist, 1945; *Ancyropenta longidenticulata*, n. sp.; *Ctenognathus gradata* (Youngquist, 1945); *Ctenopolygnathus angustidisca* (Youngquist, 1945); *Icriodus symmetricus* Branson & Mehl, 1934; *Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer, 1938); *P.* (*M.*) *foliacea* (Youngquist, 1945); *P.* (*M.*) *hassi*, n. sp.; *Polygnathus amana*, n. sp.; *P. normalis* Miller & Youngquist, 1947; *P. foliata* Bryant, 1921; *P. granulosa* Branson & Mehl, 1934; and *P. unicornis*, n. sp.

2. From a greenish gray, arenaceous, calcareous, and very fossiliferous shale in a creek bed close to the county farm near Independence, Buchanan County, Iowa, center SW¼ Sec. 25, T89N, R9W. Content: *Ancyrodella buckeyensis* Stauffer, 1938?; *A. hamata* Ulrich & Bassler, 1926; *A. gigas* Youngquist, 1947; *Ancyrognathus* aff. *A. alta*, n. sp.; *Ancyroides asymmetrica* (Ulrich & Bassler, 1926); *A. uddeni* Miller & Youngquist, 1947; *Ancyropenta longidenticulata*, n. sp.; *Ctenognathus gradata* (Youngquist, 1945); *Ctenopolygnathus angustidisca* (Youngquist, 1945); *Icriodus*

*symmetricus* Branson & Mehl, 1934; *Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer, 1938); *P.* (*M.*) *hassi*, n. sp.; *P.* (*M.*) *subrecta* (Miller & Youngquist, 1947); *P.* (*M.*) *unicornis* (Miller & Youngquist, 1947); *Polygnathus amana*, n. sp.; *P. normalis* Miller & Youngquist, 1947; *P. foliata* Bryant, 1921; *P. granulosa* Branson & Mehl, 1934; *P. independensis*, n. sp.; *P. unicornis*, n. sp.

3. From a limestone in the Independence shale at Brandon, Iowa. Content: *Ctenognathus gradata* (Youngquist, 1945); *Palmatolepis* (*Manticolepis*) *hassi*, n. sp.; *Polygnathus foliata* Bryant, 1921; *P. unicornis*, n. sp.

4. From a slightly weathered grayish brown shale at Sec. 9, T86N, R6W, in Benton County, Iowa. Content: *Palmatolepis* (*Manticolepis*) sp.; *Polygnathus normalis* Miller & Youngquist, 1947; *P. foliata* Bryant, 1921.

### SWEETLAND CREEK BEDS

The Sweetland Creek shale was named by Udden (1899) for a series of shales along Sweetland Creek, about 4 miles east of Muscatine, Muscatine County, southeast Iowa. This author lists a small macrofauna from the type section which he refers to the Upper Devonian. This opinion was maintained by Calvin (*in* Weller, 1909, p. 285) and Branson (1944, p. 159). However, Weller (1909, p. 273–274), Ulrich (1911, p. 29), Van Tuyl (1925, p. 70) Savage (1925, p. 588), and Moore (1935, p. 239–240, 245) listed the Sweetland Creek shale as tentatively belonging to the Mississippian. Wilmarth (1938, p. 2098) and Cooper et al. (1942, chart 4) placed it as either Devonian or Mississippian. Weller et al. (1948, p. 150) placed the Sweetland Creek as a synonym of the Maple Mill, in which (Laudon, 1931, p. 355) includes all of the Kinderhookian shales in southeastern Iowa.

The macrofauna in this sequence is sparse and insignificant, consisting mostly of plant remains, fish-teeth and -scales, linguloids, as well as a few poorly preserved anaptychi, which have been listed under the name *Spathiocaris emersoni* Clarke.

Branson & Mehl recognized that conodonts of these beds indicate an Upper Devonian age. In connection with the recording of two species of *Icriodus* these authors state (1938, p. 157): "The Sweetland Creek of Iowa seems to be a phase of the Grassy Creek and as the name Grassy Creek has priority, the Iowa phase may properly be called Grassy Creek." However, Sweetland Creek beds appear to correlate with the lower Grassy Creek shale only.

In two papers (Miller & Youngquist, 1947, and Youngquist & Miller, 1948) there is a detailed description of the conodont fauna from this locality. Thomas, 1950, listed additional genera and species from the lowermost bed of the same outcrop. Slight differences in composition of the faunas of the upper and lower beds are recognizable in our collections.

Lithologically the Sweetland Creek shale is a sequence of noncalcareous, greenish, dark-gray and bluish-gray, fine-grained shales with interbedded argillaceous-dolomitic layers. The presence of abraded fish teeth, particularly near the base, suggests shallow water near-shore deposition with slow sedimentation. Thickness varies between 0 and 48 feet; Sweetland Creek beds overlie the Cedar Valley with an unconformity. The uppermost part of the Cedar Valley shows signs of uneven erosion and leaching which seem to indicate that this formation had been exposed to terrestrial weathering before deposition of the Sweetland Creek shale. A coal-bearing section of the Pennsylvanian transgresses the Sweetland Creek shale unconformably, *e.g.*, at the Campbell's Run locality.

The microfauna consists of *Tasmanites*-like megaspores which are abundant in many samples. Conodonts are common and scolecodonts have also been secured. Compilations in the present report are based on the publications and type specimens of Miller & Youngquist, as well as additional collections from the same localities. The sequence at Campbell's Run was subdivided into three portions as follows:

Overlying: Pennsylvanian shale

1′6″ gray shale with *Ancyrodella buckeyensis* Stauffer, 1938; *A. hamata* Ulrich & Bassler, 1926; *A. gigas* Youngquist, 1947; *Ancyroides calvini* Miller & Youngquist, 1947; *A. princeps* Miller & Youngquist, 1947; *Ctenognathus gradata* (Youngquist, 1945); *Icriodus symmetricus* Branson & Mehl, 1934; *Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer, 1938); *P.* (*M.*) *subrecta* (Miller & Youngquist, 1947); *Polygnathus foliata* Bryant, 1921; *P. independensis*, n. sp. *P. unicornis*, n. sp.

5″ yellowish-gray shale with *Icriodus symmetricus* Branson & Mehl, 1934; *Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer, 1938); *P.* (*M.*) *hassi*, n. sp.; *P.* (*M.*)

*unicornis* (Miller & Youngquist, 1947); *Polygnathus foliata* Bryant, 1921; *P. unicornis*, n. sp.

3″ light-gray arenaceous shale with fish remains and *Ancyrognathus bifurcata* (Ulrich & Bassler, 1926); *A. triangularis* Youngquist, 1945; *Icriodus symmetricus* Branson & Mehl, 1934; *Palmatolepis* sp.; *Polygnathus foliata* Bryant, 1921.

Underlying: Cedar Valley limestone.

Not all the species described by Miller & Youngquist are represented in our collections. This lack is probably due to random distribution of the forms; the missing species seem to be rare in all cases. Not represented in our material are:

*Ancyroides? rudis* Youngquist & Miller, 1948

SUI 5586, Jour. Paleont., vol. 22, p. 442, pl. 68, fig. 19. As has been noted by Youngquist & Miller, this is a rather distinct form and its generic position is uncertain; it may belong to an undescribed genus which evolved from *Ancyrognathus* and can be distinguished by the bifid carina on the B-ward lobe. However, the holotype is the only specimen yet known, and it may be that the bifurcation is due only to abnormal growth. A similar development has been observed in a few specimens of *Polygnathus unicornis*, n. sp.

*Palmatolepis subperlobata* Branson & Mehl, 1934

SUI 5569, Jour. Paleont., vol. 21, p. 513, pl. 75, fig. 12. This specimen in our opinion belongs to an undescribed species. It resembles *Palmatolepis* (*Manticolepis*) *subrecta*, but the C-ward portion is much more strongly developed.

*Polygnathus multinodosa* Youngquist & Miller, 1948

SUI 5614, Jour. Paleont., vol. 22, p. 448, pl. 68, fig. 10. This form is close to *Polygnathus foliata* Bryant, 1921, but has a somewhat wider plate with conspicous regularly rounded nodes.

*Polygnathus carinata* Miller & Youngquist, 1947

SUI 5573, Jour. Paleont., vol. 21, p. 514, pl. 74, fig. 3. The holotype is a large fragment. The furrow in the lower part of the strongly developed blade (similar to specimen shown on Pl. 137, fig. 1b of this report) as well as the form of the A-end, seem to indicate that the specimen may be only an abnormally developed *Ancyrodella*. It seems therefore to be of little value for stratigraphic comparison.

### NORTH LIBERTY BEDS

A fine-grained, greenish-blue, noncalcareous shale is exposed about 1½ miles northeast of the village of North Liberty, Johnson County, east central Iowa.

Conodonts from this outcrop have been described by Youngquist, 1947. The locality was revisited several times in the winter of 1954, spring and summer of 1955, and spring of 1956. Within a distance of little more than half a mile (NE ¼ sec. 7 to N½ of NW¼ sec. 8, T8ON, R6W) several pockets are exposed in a small creek bed. These are not believed to be *in situ*, but pressed upward by slope slumping of the overlying drift deposits. Due to the progress of erosion, a change in size and location of these pockets has been observed. It is impossible to take well correlated samples at this locality without much digging, and the fauna secured from several pockets has to be regarded as an admixture of the entire section. Underlying the shale is a dark yellow-brownish, dolomitic, fine crystalline thin-bedded limestone which may be either basal State Quarry limestone (Stainbrook & Ladd, 1926) or uppermost Cedar Valley, as suggested by Youngquist (1947). Several samples of this bed dissolved in acetic acid have not yielded a single conodont.

Youngquist's type specimens as well as our more abundant and better preserved collections contain a number of species which are not present at the Amana, Sweetland Creek, or Independence localities. With reservation, some of them (*Icriodus latericrescens*, *I. expansus*, and *Palmatolepis* (*Manticolepis*) *martenbergensis*) are considered to be somewhat older than the rocks exposed at Amana, Independence, and Muscatine. However, the bulk of the species represented occur also in the Amana, and Sweetland Creek, as well as in the Independence beds.

Of the species described by Youngquist, 1947, the following were not observed in our collection:

*Polygnathus spatulata* Youngquist, 1947

SUI 4054, Jour. Paleont., vol. 21, p. 110, pl. 26, fig. 4. The only specimen, the holotype, is missing and neither description nor figure allow us to recognize this species; therefore, it seems impossible to use it for stratigraphic comparison.

*Polygnathus percarinata* Youngquist, 1947

SUI 4052, Jour. Paleont., vol. 21, p. 109, pl. 24, fig. 1. The plate is little arched, its rim much higher than the portion beside the carina which has elongate troughs. Sculpture consists of ridges, perpendicular to the rim. Carina meets the B-ward tip. A large portion of the blade is not preserved on the type. Specimens from the

Sweetland Creek beds, previously determined as *Polygnathus webbi*, may belong to this species.

*Icriodus latericrescens* Branson & Mehl, 1938 Jour. Paleont., vol. 12, p. 164, pl. 26, fig. 30–37, [lectotype designated by Ziegler (1956, p. 100) is original of fig. 33]. SUI 3386, Jour. Paleont., vol. 21, p. 102, pl. 25, fig. 12. This species has been found in the Lower and Middle Devonian. In the earliest Upper Devonian Genundewa, it is probably an admixture. Its occurrence in the North Liberty beds, if not also due to reworking, may have significance for determination of the beginning of shale sedimentation in this area.

### SINKHOLE FILLING IN THE CEDAR VALLEY LIMESTONE AT SOLON

In an old quarry, a quarter of a mile west of Solon, Johnson County, Iowa, NE¼ Sec. 26, T81N, R6W, a sinkhole is exposed within the limestone of the Rapid member of the Cedar Valley formation. The shales within this sinkhole are distinctly bedded, gray, greenish or black, and in some layers arenaceous. One of the light-colored, noncalcareous, fine-grained shales near the top of the outcrop has produced a conodont fauna containing several species which are regarded as diagnostic for the Independence fauna. However, the material is only fragmentary and not sufficiently well preserved for a detailed study. It contains *Ancyrodella buckeyensis* Stauffer, 1938; *Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer, 1938); *P.* (*M.*) *hassi*, n. sp.; *Polygnathus foliata* Bryant, 1921.

Youngquist (1947, p. 202) has listed *Icriodus postiflexus* Branson & Mehl and *Hindeodella* from shale partings in the same quarry. The species cited has been correctly referred to the Cedar Valley formation and is absent in the Independence fauna.

## FACIES DIFFERENCES BETWEEN THE AMANA, INDEPENDENCE, SWEETLAND CREEK, AND NORTH LIBERTY BEDS

Although the conodont assemblages secured from all these localities are similar, there are remarkable differences in the other fossils. Amana and Independence beds contain abundant and somewhat different macrofauna. According to Stainbrook (1945, p. 7):

> *Hystricina, Douvillinaria, Douvillina, Nervostrophia, Atrypa*, and *Lingula* occur in both the Independence and Amana beds but are represented by distinct species. These genera—*Macgeea, Charactophyllum, Petrocrania, Skenidium, Schuchertella, Schizophoria, Calvinaria, Pugnoides, Aullacella*—indicate similarity to the Independence as they are represented in each by the same or varietal forms. Distinctness of the two terranes is shown by these Independence genera which do not occur in the Amana beds: *Metriophyllum, Cyphaspis, Ponticeras, Cariniferella, Chonetes, Sulcatostrophia, Camarotoechia, Strophalosia, Devonoproductus, Hypothyridina, Grünewaldtia, Cyrtospirifer, Thomasaria*, and *Acutatheca*. Further *Manticoceras, Tornoceras*, and *Platyceras* are found in the Amana beds but not in the Independence. . . . preliminary study indicates that the Amana beds and their fauna are intermediate between the Independence and the Lime Creek.

The presence or absence of long ranging genera and species seems to us only a result of slight differences in facies.

Lithologically the Independence shale is more calcareous than the main part of the Amana beds. Only the layers above the middle of the section at State Highway 220 are lithologically similar to the beds at the county farm near Independence. The upper portion of the Amana section consists mainly of noncalcareous shales, which are not exposed at the nearby county farm.

In their composition the microfaunas are also somewhat different. Ostracodes are abundant at the Independence localities but sparse and restricted to the few most calcareous layers in the Amana beds. *Tentaculites* is widespread near Independence, but is restricted to the few more calcareous feet at Amana. Holothurian spicules are common and well preserved in the Independence locality in the creek bed, but they have not been found in the Amana beds. Conversely, scolecodonts are more common in the Amana beds, particularly in their upper portion.

The Sweetland Creek beds have still less calcareous components than the Amana beds as a whole. They are more arenaceous and contain many scolecodonts and commonly plant remains, which have not been observed at Amana and are rare at the county farm near Independence. At the type locality of the Independence, plant remains are reported to have been common. Due to the poor exposures it was impossible to secure any conodonts from this locality.

The North Liberty beds allow few gen-

eralizations, for they are poorly exposed. Our samples have yielded only a few plant remains and no calcareous fossils.

The Sweetland Creek beds seem to have been deposited near shore, and the Independence sections in a shallow sea somewhat offshore; the Amana beds may have been intermediate. The nectonic conodonts, however, did not depend on the bottom conditions and are distributed with the same forms regardless of these differences in facies.

## COMPARISON WITH OTHER DEVONIAN FORMATIONS

*Cedar Valley limestone.*—In accordance with Cooper & Warthin (*e.g.* 1942, p. 1737) this sequence of limestones with abundant and well preserved brachiopods and corals is regarded as older than the Independence formation. Its fauna is characterized by forms like *Polygnathus linguiformis*, *Icriodus expansus*, and *I. latericrescens*, which clearly are older than the bulk of Independence conodonts. Only at the North Liberty locality have representatives of some of these species been secured from a shale. However, all characteristic species of the Independence formation are lacking in the Cedar Valley

*Lime Creek formation.*—The age of these beds is determined to be early Upper Devonian by the goniatite *Manticoceras regulare* Fenton & Fenton. As was demonstrated in middle Europe, at this time ostracodes (Rabien, 1954) as well as conodonts seem to be even more time sensitive than goniatites. Utilizing these fossils, it is possible to subdivide the classic Adorf-Stufe into several zones. It seems that conodonts have the same potentialities in Iowa also.

However, our collections from Bird Hill and Juniper Hill are small, and the beds are now being studied by other investigators with more and better material. Therefore, it now seems inadvisable to express an opinon whether the Lime Creek is older or younger than the Independence.

*Maple Mill shale.*—This formation is characterized by forms like *Palmatolepis* (*Palmatolepis*) *perlobata*, *P.* (*P.*) *glabra*, and *Pelekysgnathus* sp. These forms are younger than the Independence formation. Although the Maple Mill contains some forms which have not yet been found in Europe, it may be stated that the general appearance of this fauna suggests an age not younger than the *Platyclymenia*-Stufe.

From a bonebed horizon, a few feet beneath the top of the Maple Mill shale at the type locality, we secured a large quantity of Middle Devonian conodonts which obviously are reworked. It is suggested that part of the material described by Thomas, 1949, from these beds, *e.g.*, *Polygnathus linguiformis* Hinde (=*P. sanduskiensis* Stauffer) are in secondary deposit.

*Grassy Creek shale*—This formation in Missouri includes equivalents of the Independence formation, as well as of the Maple Mill shale. Furthermore, it comprises beds which are not described from Iowa. For example, part of Branson & Mehl's collections from the Monroe City, Missouri, locality may be younger than the Maple Mill.

*Sheffield shale.*—From these beds in north-central Iowa, we secured a highly advanced species of *Palmatolepis* (*Manticolepis*). *Icriodus* is prevalent in this association with species which have no equivalent in the Grassy Creek. They may be of uppermost *Manticoceras*-age or a little younger.

*Arkansas novaculite.*—As is noted on a prior page, collection 412 of Hass (1951) from the middle zone of the Arkansas novaculite at Caddo Gap, Montgomery County, Arkansas, is regarded as an equivalent of the Independence fauna.

*Olentangy shale.*—Part of the Olentangy shale conodonts described by Stauffer, 1938, are identical with those of the Independence formation.

If the occurrence of identical conodont species in North America and Europe can be regarded as evidence for contemporaneous deposition of the containing beds, the correlation indicated may be made.

### ZONATION OF THE INDEPENDENCE FORMATION

Some forms seem to be suitable for a zonation within the Independence formation. The genus *Ancyroides* is restricted at Amana to the upper portion of the exposure, beds 8–12; and *Palmatolepis* (*Manticolepis*) *subrecta* to beds 10–13, where it is abundant. Both are also common in the Sweetland Creek shale. Conversely, *Palmatolepis*

TABLE 1—CORRELATION OF UPPER DEVONIAN BASED ON CONODONTS

| Middle Europe | | United States |
|---|---|---|
| Wocklum (*Wocklumeria*) Stufe | | |
| Dasberg (*Oxyclymenia*) Stufe | | |
| Hemberg (*Platyclymenia*) Stufe part of Famennian | | part of Grassy Creek shale, Maple Mill shale, part of middle New Albany shale |
| Nehden (*Cheiloceras*) Stufe part of Famennian | | Gassaway member of Chattanooga shale? Sheffield shale? |
| Adorf (*Manticoceras*) Stufe Frasnian | Upper | Independence formation, Lime Creek formation, part of Grassy shale |
| | Middle | Rhinestreet shale, parts of Independence formation at North Liberty |
| | Lower | Squaw Bay limestone, Genundewa limestone |

(*Manticolepis*) *foliacea* is abundant in beds 1–8 at Amana; it is lacking in the upper layers and has not been found in the Sweetland Creek shale. The North Liberty beds contain the less advanced species of the assemblages studied in this report: *Icriodus latericrescens*, *I. expansus*, and *Palmatolepis* (*Manticolepis*) *martenbergensis*, which have not been found elsewhere in the Independence formation.

Miller & Youngquist (1947, p. 502) state for their Sweetland Creek material: "The conodant fauna . . . appears to be somewhat more advanced than those described . . . in 1945 and 1947 from the Upper Devonian beds near Middle Amana and North Liberty, Iowa." This statement is in accord with our conclusions, insofar as the previous studies comprised material from only the lower portions of the Amana section.

The Independence shale, at the cross road of the county farm locality, has yielded a

EXPLANATION OF PLATE 135

All specimens are from the Amana beds at State Highway 220 near Middle Amana, Iowa Co., Iowa. All figures are unretouched photographs, ×40.

FIG. *1*—*Polygnathus foliata* Bryant. Sinistral specimen; *a*, lateral view (from D) with part of the base; *b*, upper view. Layer 6.

*2,8*—*Polygnathus granulosa* Branson & Mehl. *2*, sinistral specimen; *a*, upper view; *b*, lateral view (from D), demonstrates the fan-shaped growth lines on the blade. Layer 8. *8*, dextral, large specimen, demonstrates the *linguiformis*-pattern; *a*, upper view; *b*, lower view with crimp and small escutcheon. Layer 7. (See also Pl. 141, fig. 1.)

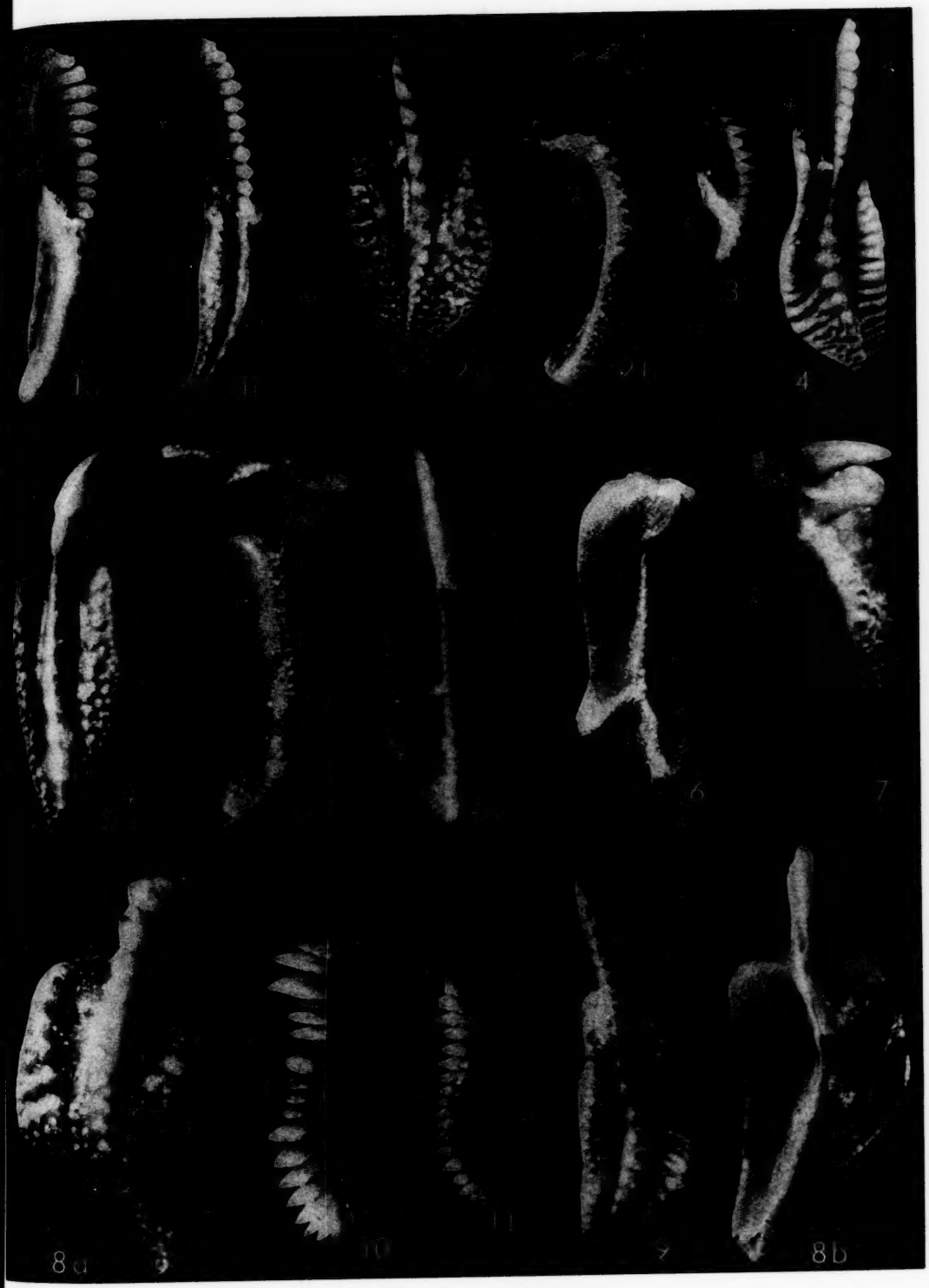
*3*—*Polygnathus* sp. Lateral view of a small specimen for comparison with the arched B-ward portion of *Ctenognathus*. Layer 7. (State Univ. Iowa, 9914.)

*4*—*Polygnathus amana*, n. sp. Holotype, dextral, upper view. Layer 11.

*5–7*—*Polygnathus unicornis*, n. sp. *5*, holotype, dextral; *a*, upper view; *b*, lateral view (from C); *c*, lower view. Layer 6. *6*, sinistral specimen, lower view; the blade is not preserved; the secondary keel is regarded as due to abnormal growth. Layer 7. *7*, paratype, dextral, lateral view (from C), has a bisected large denticle on blade. Layer 7. (See also Pl. 141, fig. 10.)

*9*—*Polygnathus normalis* Miller & Youngquist. Sinistral specimen, upper view. Layer 9. (See also Pl. 141, fig. 3.)

*10,11*—*Ctenognathus gradata* (Youngquist). *10*, large specimen with regeneration of some denticles in the middle portion. Layer 7. *11*, specimen demonstrates germ denticles. Layer 3.


8a
8b

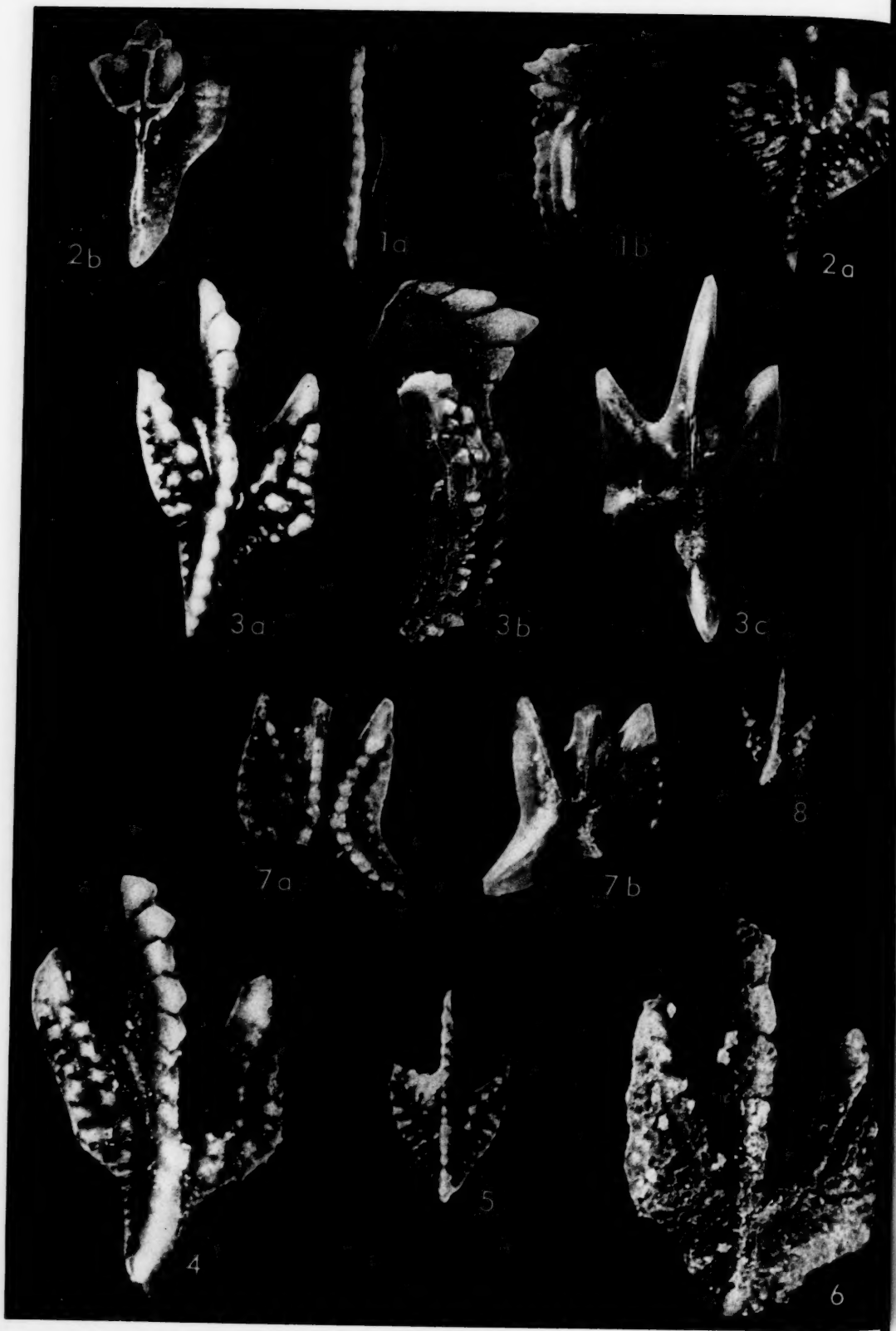

2b
1a
1b
2a
3a
3b
3c
7a
7b
8
4
5
6

TABLE 2—ZONATION OF THE INDEPENDENCE FORMATION ON THE BASIS OF CONODONTS

| AMANA BEDS | SWEETLAND CREEK SHALE | INDEPENDENCE SHALE | NORTH LIBERTY BEDS |
|---|---|---|---|
| *Ancyroides*<br>*Palmatolepis subrecta* | *Ancyroides*<br>*Palmatolepis subrecta* | *Ancyroides*<br>*Palmatolepis subrecta* | — |
| *Palmatolepis foliacea* | — | *Palmatolepis foliacea* | *Palmatolepis foliacea* |
| — | — | — | *Palmatolepis martenbergensis*<br>*Icriodus expansus*<br>*Icriodus latericrescens* |

fauna containing *Palmatolepis* (*Manticolepis*) *foliacea* but without *Ancyroides* and *Palmatolepis* (*Manticolepis*) *subrecta*. This collection may well correlate with the Amana beds 1–8. Conversely the small outcrop at the nearby creek bed has yielded an association with *Ancyroides* and abundant *Palmatolepis* (*Manticolepis*) *subrecta*. Therefore, this layer correlates approximately with the upper beds of the Amana locality.

Presence or absence of one or the other zones in the individual sequences may be due to poor exposure. Therefore, without further detailed studies in the field it is not advisable to use these findings for reconstruction of paleogeography. However, these zones may eventually be used for plotting the transgression of the early Upper Devonian sea over the Cedar Valley limestone.

Little can be said on the possibilities of tracing these zones over a wider area. *Ancyroides* and species similar to *Palmatolepis* (*Manticolepis*) *subrecta* are widely distributed in North America, Europe, and Australia. However, the conspicuous *Palmatolepis* (*Manticolepis*) *foliacea* has not been found outside of the beds described here.

## METHODS FOR PREPARATION

Conodonts have been secured from limestone as well as shale samples. The limestone was crushed to pieces of about one inch diameter, and dissolved in 15% acetic acid. The standard size of a sample for preliminary examination was 500 gm. Beds which yielded the best conodont associations were then resampled. Up to 16 kg. of an individual bed have been processed, so that most of the representation may be expected in these collections.

The shales have been prepared with the kerosene method, described by Crowley (1952) and Redmond (1953). The residues were not too bulky to be picked without a preceding separation with heavy liquids. For illustration, the specimens have been coated lightly with magnesium oxide and then photographed with a pin-hole camera.

### EXPLANATION OF PLATE 136

All specimens are from the Amana beds at State Highway 220 near Middle Amana, Iowa Co., Iowa. All figures are unretouched photographs, ×40.

FIG. *1*—*Ctenopolygnathus angustidisca* (Youngquist). *a*, upper view; *b*, lateral view. Layer 9.
*2*—*Ancyrodella buckeyensis* Stauffer. Sinistral, large specimen, the blade is not preserved; *a*, upper view; *b*, lower view. Layer 8.
*3*—*Ancyropenta longidenticulata*, n. sp. Sinistral specimen; *a*, upper view; *b*, lateral view (from D); *c*, lower view. Layer 8. (See also Pl. 137, fig. 1,2.)
*4*—*Ancyrodella hamata* Ulrich & Bassler, Sinistral specimen, upper view. Layer 7.
*5*—*Ancyrodella buckeyensis* Stauffer. Upper view of small specimen. Layer 8.
*6*—*Ancyrodella subrotunda* Miller & Youngquist. Sinistral, upper view of large specimen. Layer 7.
*7,8*—*Ancyropenta asteroideus* (Stauffer). *7*, sinistral, large fragment; *a*, upper view; *b*, lower view. Layer 8. *8*, sinistral, small specimen. Layer 8.

A more detailed account of these techniques for preparation and photography has been given previously (Müller, 1956a).

## REMARKS ON THE ASSOCIATED MICROFAUNA

The Independence and associated beds have yielded a variety of other microfossils.

*Megaspores.*—Spore-like bodies, *Tasmanites* (Pl. 142, fig. 7), are abundant, particularly in the Sweetland Creek beds, the upper portion of the Amana section, and in one collection from the North Liberty locality. In some cases practically the entire washed residue of a shale sample consists of these fossils, compressed and poorly preserved. The same type of spores has been secured also from a number of Grassy Creek shale samples. *Tasmanites huronensis* (Dawson) as figured by Ellison (1950, p. 12, pl. 3, fig. 5,6,8) from a subsurface sample of the Woodford shale in West Texas is similar and possibly identical with these findings.

*Hystrichosphaeridae.*—Hystrichosphaerids are fairly common in the Amana as well as the Independence beds. After dissolving limestones in diluted acid many specimens may be secured by filtration of only the clear part of the solution on which they are floating. Hystrichosphaeridae may then be picked directly from the wet filter under the microscope.

*Foraminifera.*—Foraminifers occur at the Independence and Amana localities, but have not been found in the Sweetland Creek and North Liberty sections. The foraminifers of the Independence shale have been described by Cushman & Stainbrook (1943) who have recorded the following genera and species: *Rhabdammina* sp.; *Saccammina*? sp.; *Proteonina pseudospiralis* Cushman & Stainbrook, 1943; *Hyperammina* (?) sp.; *Lituotuba dubia* Miller & Carmer, 1933; *Endothyra gallowayi* Thomas, 1931; *Semitextularia thomasi* Miller & Carmer, 1933; *Textularia? proboscidea* Cushman & Stainbrook, 1943; and *Pseudopalmula palmuloides* Cushman & Stainbrook, 1943.

*Tentaculites.*—An undescribed species of *Tentaculites* is common at both collecting points at the county farm near Independence and in the calcareous beds 3 and 5 of the Amana section.

*Scolecodonts.*—These fossils are not common, in contrast to the other Devonian formations of the Iowa section. In the Sheffield and Maple Mill shales they are plentiful and well preserved. Our collections from the Sweetland Creek, and North Liberty localities include about 50–60 specimens.

*Holothurian spicules.*—Sieve plates, which may be regarded as remains of Holothuria, are common and well preserved at both collecting localities near Independence.

*Ostracodes.*—Abundant in both outcrops at the county farm near Independence and fairly common in bed 3 at Amana.

*Fish remains.*—Teeth and scales are widespread but uncommon in the shales and limestones. Mr. W. Gross of Berlin has determined material secured from bed 7 at Amana as belonging to the following genera: *Protacrodus*, *Phoebodus*, *Onychodus*, and unrecognizable genera of Acanthodii. The North Liberty locality has yielded mainly *Ptyctodus*.

## GENERAL APPRAISAL OF THE CONODONT FAUNA

The fauna under consideration consists of a large variety of form-types. The platform types alone represent 9 genera with 34 species. This abundance reflects the fact that in the early Upper Devonian the development of conodonts was at its height. Furthermore, many of the rarer partial-species would not have been found in smaller collections.

Regenerations of broken denticles are not rare. Also, because of the excellent preservation in some beds, the growth lamellae, even of basal parts, are readily visible. The average size of the conodonts is larger than in other occurrences of the same age. This may be an indication of favorable living conditions for the conodont animal. The exceptionally large dimensions of some highly advanced forms, for example *Ancyropenta longidenticulata* and *Ancyroides iowaensis*, may be due to an increase in size during evolution, as observed in other groups of fossils.

There is no appreciable difference in composition of the fauna in the shale and the limestone beds. However, it may be stated that abundance as well as quality of preservation in certain limestone layers exceeds that of all shale beds. This greater abundance may be due to the slower rate of sedi-

mentation in the limestones, and to lesser diagenetic alteration.

*Palmatolepis* is the prevalent conodont. This genus makes up as much as 50% of the entire association secured from an individual bed. As was demonstrated in Europe, species of *Palmatolepis* are excellent time markers. All species of the Independence formation belong to the subgenus *Manticolepis* which seems to be restricted to early Upper Devonian.

Although not as common as *Palmatolepis*, the partial-genus *Ancyroides* is regarded as a good index fossil also. It seems to be restricted to the upper part of the *Manticoceras*-Stufe. In the Amana section the genus is confined to the higher beds. Conspecific forms of this genus are distributed over America, Europe, and Australia.

The partial-genera *Ancyrodella*, *Ancyrognathus*, and *Ancyropenta* are represented in the fauna with highly developed forms, and in some cases are conspicuously large. *Polygnathus* is abundant in some layers; this genus is long ranging but has produced diagnostic and short-lived species. *Ctenognathus* and *Ctenopolygnathus* are regarded as having less significance in stratigraphy. *Icriodus* is rare and represented by only two species. This rarity may be due to environmental factors for the same genus has been found abundantly in other sediments of approximately the same age.

We have not studied yet the bar and blade types. It seems that among these form-types there are also good index fossils.

## CONCEPT OF PARTIAL-SPECIES

For reasons which have been discussed in a previous paper (Müller, 1956b, p. 1330) it is believed that the concept of species in conodonts has to be drawn broadly. Therefore, we have not hesitated to associate species names in all cases where it is impossible to draw a differential diagnosis between the similar forms from previous descriptions or examination of the type specimens—examination of type specimens from previous papers is marked in the synonymy by a preceding "*v.*" In many cases, much larger or smaller specimens cannot be recognized as belonging to the same species, if only the holotype is known. In such cases supplementary personal collections from type localities of previous authors proved to be useful for comparisons.

## GLOSSARY

Comparative study of partial-species, the basis of stratigraphic application in conodonts, demands proper description of all features which may have changed in the course of evolution. The following glossary is especially modeled for the Polygnathidae, but some of the features may also be useful for characterization of species in other groups. Consistent description of the details on all species may add to the knowledge of evolution and will certainly facilitate comparisons.

*ABCD*—symbols for artifical orientation of conodonts; see Müller, 1956b, p. 1331.

*Apex*—culmination point of carina and secondary carina(e). It is in most cases, but not necessarily, in the growth-center.

*Arching*—refers to a bending only in the vertical direction.

*Azygous node*—large denticle on the upper side of plate in the growth-center; its equivalent in some cases is visible on the lower surface (*e.g.*, on *Palmatolepis*).

*Basal portion*—part of the lower side which has not been covered by the conodont forming tissue.

*Blade*—high, strongly developed portion, Award of the carina.

*Bowing*—refers to bending or curving laterally (toward C or D).

*Carina*—ridge on the upper surface of platform in the longitudinal growth axis, and corresponding to the keel.

*Crimp*—overlapping part of lower side which has been covered by the same tissue as the upper side; it is often distinct by a shinier surface.

*Discrete*—separate (antonym of fused).

*Escutcheon*—(redefinition) a rudiment of the basal cavity of more primitive conodonts; (*e.g.*, Distacodidae). Its position is beneath the growth center.

*Flange*—enlargement on the sides of blade types. It may be the nucleus from which phylogenetically the plate was developed.

*Free blade*—portion of blade, not flanked by the plate.

*Fused*—refers to denticles which are grown together; in some cases with exception only of the tips (antonym of discrete).

*Germ denticle*—denticle which is overgrown by adjacent denticles. Often it is visible only in transmitted light.

*Growth center*—center of the growth lines.

*Growth lamellae*—layers which compose the conodont (visible in cross sections).

*Growth lines*—(striae) fine lines on the lower

side of many conodonts (platform as well as bar types) which are formed by the edges of the growth lamellae.

*Keel*—a sharp ridge on the lower side which corresponds to blade and carina. It is often composed of two leaves.

*Keel angle*—the angle between the B-ward portion of keel and secondary keels, measured near the apex. The angle between secondary carinae is essentially the same (*e.g.*, in *Ancyrognathus*, *Ancyroides* and *Ancyropenta*).

*Lobe*—a projection of the plate which may have a carina or secondary carina in its center.

*Lower side*—conventionally regarded as the side with the growth striae, keel, and crimp.

*Plate*—more or less flat part of conodonts extending on the sides of the carina, and often adorned with a sculpture. In Polygnathidae this feature has been developed from the flanges of *Ctenognathus*, as it is suggested by *Ctenopolygnathus*.

*Rim*—outline of the plate. This feature may change considerably in course of ontogeny.

*Sculpture*—nodes or small ridges on the upper surface of plate which are built up layer by layer from the upper side and often change their pattern during ontogeny. The pattern of arrangement in transverse, longitudinal, or concentric rows or ridges is of some importance for taxonomy.

*Secondary carina*—a sharp ridge on the upper side of plate, ±perpendicular to the carina. It corresponds to the secondary keel.

*Secondary keel*—a sharp ridge on the lower side which branches off from the keel and corresponds to a secondary carina. In some cases it is present only at the tip of the lobes, evidence that it has been developed only in larger growth stages (*e.g.* in *Palmatolepis*, *Ancyrodella*, *Ancyropenta*, *Ancyroides*).

*Secondary keel angle*—the angle between secondary keels (on A-side) measured near the apex. The angle between secondary carinae is essentially the same. However, irregularities in arrangement of denticles in some species often prevent accurate measurement of the angle from the upper side (*e.g.*, in *Ancyrodella* and *Ancyropenta*).

*Sinus*—an indentation in the rim of plate between adjacent lobes.

*Slant*—pitch of blade on its A-ward tip.

*Suture*—line between upper side of the conodont including crimp, if present, and the basal portion.

*Trough*—depression on one or both sides of the blade on A-portion of plate. It is deepest on the A-limit and tapers toward the center of the conodont. The trough is distinguished from the plate by lack of sculpture. (On *Polygnathus*, *Ancyrodella*, *Palmatolepis*, *Ancyropenta*, *Ancyrognathus*, *Siphonodella*, etc.).

*Upper side*—conventionally regarded as the side with the denticles of blade and carina as well as sculpture of plate. It consists of the last deposited growth lamella.

## SYSTEMATIC DESCRIPTIONS

### Genus CTENOGNATHUS Pander, 1856

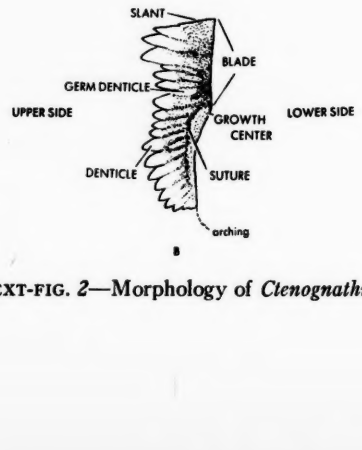
*Ctenognathus* PANDER, 1856, Russ. Balt. Gouvernements, p. 32.
*Prionognathus* PANDER, 1856, ibid., p. 34.
*Spathodus* BRANSON & MEHL, 1933, Univ. Missouri Stud., vol. 8, p. 46.
*Pandorina* STAUFFER, 1940, Jour. Paleont., vol. 14, p. 428.
*Spathognathodus* BRANSON & MEHL, 1941, ibid., vol. 15, p. 98.
*Mehlina* YOUNGQUIST, 1945, ibid., vol. 19, p. 363.

Type species.—*Ctenognathus murchisoni* Pander.

*Diagnosis* (redefinition).—Compound ±asymmetrical, blade-like conodonts with more or less developed flanges which are never sculptured. The upper side is denticulated in its entirety. Blade and denticles are higher in the A-portion and decreasing toward B. Germ denticles and/or flanges may be present. The B-portion of the lower limit is in most cases somewhat arched, and the A-portion either straight or also arched, thus forming a more or less distinct, obtuse angle at the junction. The basal cavity differs widely in size and depth, in a few species it is not reduced at all.

*Subdivision.*—Stauffer (1940, p. 428) had established a genus *Pandorina* for forms which are similar to the typical *Ctenognathus* but have a large basal cavity ("notch") on the B-portion. The tendency of increasing the size of basal cavity in some *Ctenognathus* had led to the Gnathodontidae. The feature may be utilized for recognition of a subgenus within the large number of species in this partial-genus.

However, *Pandorina* was preoccupied by J. B. Bory, 1826, and is to be replaced by




TEXT-FIG. 2—Morphology of *Ctenognathus*.

*Pandorinellina*, n. name. Wilbert Hass has informed us that he had plans to use it in his forthcoming contribution to the *Treatise of Invertebrate Paleontology*, and the name should be attributed to him.

*Recorded range.*—Silurian-Triassic.

### CTENOGNATHUS GRADATA (Youngquist)
Pl. 135, fig. 10–11

v. *Mehlina gradatus* YOUNGQUIST, 1945, Jour. Paleont., vol. 19, p. 363, pl. 56, fig. 3 [=holotype].
v. *Mehlina irregularis* YOUNGQUIST, 1945, ibid., pl. 56, fig. 2.

*Diagnosis.*—A representative of *Ctenognathus* with nearly straight axis. Denticles subregular, germ denticles are developed. Without flanges. Basal cavity only small.

*Description.*—Axis straight or little bowed (convex toward C). Denticles subregular, long, laterally compressed and partly fused, largest are B-ward of the A-tip. On some specimens a few denticles are broken and regenerated; or are somewhat smaller in size than the unbroken denticles (Pl. 135, fig. 10). This feature has been regarded to constitute *Mehlina irregularis* but in our opinion does not justify taxonomic separation. Germ denticles are visible on every specimen. Lower limit is formed by two arches, the one in A-ward portion is less pronounced than the B-ward one. The escutcheon is rudimentary. No flanges are developed.

*Comparison.*—*Ctenognathus strigosus* (Branson & Mehl, 1934) is similar but has more denticles in comparable growth stages, and not as well developed arches on lower limit.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 3,4,6–8,11. Independence shale at the county farm near Independence, outcrops at the crossroad and in the creek bed. Limestone bed in Independence shale at Brandon. Sweetland Creek shale near Muscatine, upper layer at Campbell's Run.

*Figured specimens.*—SUI 9923, SUI 9924; unfigured specimen SUI 9986.

### CTENOGNATHUS (PANDORINELLINA) INSITA (Stauffer)
Pl. 142, fig. 2,3

*Pandorina insita* STAUFFER, 1940, Jour. Paleont., vol. 14, p. 429, pl. 59, fig. 23,25. [25=lectotype designated here].
*Pandorina gratiosa* STAUFFER, 1940, ibid., p. 428, pl. 59, fig. 18–20,24.
v. *Spathognathodus gratiosus* YOUNGQUIST, 1947, Jour. Paleont., vol. 21, p. 111, pl. 26, fig. 1.

*Diagnosis.*—A representative of *Ctenognathus* with a high A-ward portion; its large denticles somewhat reclined toward B, and with an arched B-portion. The basal cavity is fairly large.

*Description.*—Axis straight or a little bowed (convex toward C). Denticles on A-ward portion large, irregular in size and fused, except the tips. Germ denticles are rare. The general direction of the largest denticles in the A-portion is slightly toward B. This feature, however, on large specimens is no longer visible. B-portion ±strongly arched and adorned with subregular large denticles. Lower limit consists of two distinct arches which meet about ⅓ of the length of unit behind the A-ward tip. Basal cavity long and narrow, fairly large. Flanges rudimentary.

*Occurrence.*—North Liberty beds 1½ miles northeast of North Liberty (probably from the lower part). Originally described from upper part of Cedar Valley limestone, Hickok quarry, LeRoy, Minnesota.

*Figured specimen.*—SUI 9976, SUI 9977.

### Superfamily POLYGNATHACEAE Müller & Müller, n. superfam.

Under this name are united those form types which have been evolved from *Ctenognathus* by development of a plate. The more or less pronounced blade and carina are adorned with a row of ±approximated nodes. Included are the Polygnathidae Ulrich & Bassler, 1925, Gnathodontidae Branson & Mehl, 1944, and Icriodidae, n. fam.

### Family POLYGNATHIDAE Ulrich & Bassler

*Diagnosis.*—(After Ulrich & Bassler, 1926, p. 43.) Plates with a high denticulated median or lateral crest which is often extended stalklike from one end.

(After Branson & Mehl, 1944, p. 244.) Dental units leaflike plates, fundamentally bilaterally symmetrical; a median blade extends forward from plate; aboral surface with small attachment scar in middle of plate.

(New definition.) Paired, platformlike conodonts with a well developed blade, part

of which is free. Lower side has a crimp and only a small escutcheon which is homologous to the basal cavity in other families. In some groups the escutcheon is reduced to a node. Carina is present, one or more secondary carinae may be developed.

*Remarks.*—This group has derived from *Ctenognathus* in a fashion as is suggested by *Ctenopolygnathus*. The subcentral position of escutcheon and the arching of B-portion of the unit are primitive features, which remain unaltered in most of the genera belonging to this family.

To the diagnosis of Branson & Mehl the following change is proposed: fundamentally bilaterally symmetrical has to be omitted, for partial-genera like *Palmatolepis* and *Ancyroides* demonstrate asymmetry.

Many *Ctenognathus* and the most primitive species of *Polygnathus* have bilateral symmetry and possibly were arranged in the main axis of the body of the conodont animal. However, more advanced forms of these genera occur in pairs forming dextral and sinistral specimens.

The Polygnathidae belong to the best index fossils in Devonian and Early Mississippian, where they are abundant.

*Recorded range.*—Devonian-Mississippian.

## Genus CTENOPOLYGNATHUS Müller & Müller, n. gen.

Type species.—*Polygnathus angustidisca* Youngquist, 1945.

*Derivatio nominis.*—Composed from *Ctenognathus* and *Polygnathus*, because the genus is morphologically intermediate.

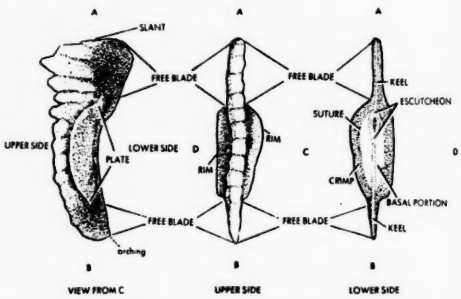
*Diagnosis.*—A representative of Polygnathidae with prominent free blade which is developed on both sides of the plate, but is somewhat longer toward A. The carina may increase in height toward both ends. The ±small plate is higher at the rim than near the blade and may be sculptured. The crimp is broad; an escutcheon is present; germ denticles are common.

*Remarks.*—*Ctenopolygnathus* has features of *Ctenognathus* as well as of *Polygnathus*. However, since *Polygnathus* is represented in Lower Devonian and the first known *Ctenopolygnathus* is Upper Devonian this form may not be the ancestor of *Polygnathus* but a different branch of evolution.

To *Ctenopolygnathus* belong the following species:

*Polygnathus brevilamina* Branson & Mehl, 1934 (the type to Pl. 21, fig. 3 is designated lectotype of this species), v. *Polygnathus cunulae* Youngquist & Patterson, 1949; v. *Polygnathus iowaensis* Youngquist & Peterson, 1947; *Polygnathus omala* Cooper, 1939; *Polygnathus oxys* Cooper, 1939; *Polygnathus perplana* E. R. Branson, 1934; v. *Polygnathus postbrevicornis* Youngquist & Peterson, 1947; v. *Polygnathus subtortilis* Youngquist & Patterson, 1949; *Polygnathus toxophora* Cooper, 1939; *Polygnathus xyncha* Cooper, 1939.

*Recorded range.*—Upper Devonian—Lower Mississippian.




TEXT-FIG. 3—Morphology of *Ctenopolygnathus*.

## CTENOPOLYGNATHUS ANGUSTIDISCA (Youngquist) Pl. 136, fig. 1a,b

v. *Polygnathus angustidiscus* YOUNGQUIST, 1945, Jour. Paleont., vol. 19, p. 365, pl. 54, fig. 2, [=holotype].

*Diagnosis.*—A *Ctenopolygnathus* with a high blade on the A-side, and strongly arched B-portion. The plate is unsculptured.

*Description.*—Blade nearly straight, on A-side very high, the highest point is near A. Denticles are large, germ denticles not very prominent; toward B the denticles are more or less fused and decrease in height. The B-portion of the blade is shorter than the A-portion. Plate subsymmetrical, on rims higher than near the blade, and unsculptured. Lower side: crimp broad, keel nearly straight, escutcheon relatively large and elongate.

*Remarks.*—On *Ctenopolygnathus iowaensis* the B-portion is not arched and the blade is somewhat curved. On *Ctenopolygnathus*

*decorosa* the B-portion of blade is considerably smaller and the plate is more ornate.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 3,5,9. Independence shale at the county farm near Independence, outcrops at the crossroad and in the creek bed.

*Figured specimen.*—SUI 9925.

### Genus POLYGNATHUS Hinde, 1879

Type species.—*Polygnathus dubia* Hinde, 1879 (designated by Miller, 1889, p. 520).

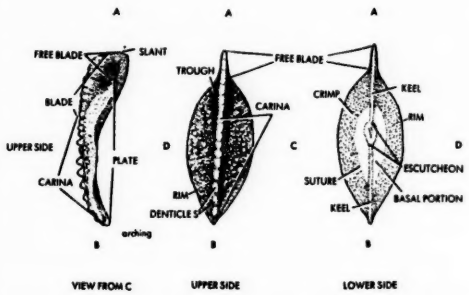
*Remarks.*—In the original description Hinde (1879, p. 362) has established this genus for a number of units which have been preserved on the same slab of Genesee shale and which he believed to be a natural assemblage. His point of view may need revision, and a restudy of his type material is necessary. If Hinde's specimen proves to be a natural assemblage, the partial-genus as defined by Bryant (1921, p. 23) would have to be renamed. In the light of our limited knowledge of assemblages it seems unlikely that two so widely different species of *Hindeodella*, as represented by his fig. 13 and 14 on Pl. 16 could have belonged to the same animal. Therefore, the name *Polygnathus* is retained here in the restricted sense of Bryant, and Hinde's original to Pl. 16, fig. 17 is accepted as lectotype of the type species.

*Diagnosis.*—(After Ulrich & Bassler, 1926, p. 43.) Plate subsymmetrically lanceolate, traversed by a high median carina extending stalklike from the broader end and reaching, although diminishing gradually in height, to the opposite usually pointed end, dividing the plate into two lateral, subequal areas. The carina is also indicated by a corresponding ridge on the underside. On the upper surface the summit of the carina carries a row of closely approximated nodes and the depressed sides of the plate are variously ornamented with nodose ridges. The underside is smooth or has fine concentric lines.

(After Branson & Mehl, 1944, p. 245.) Dental unit a transversely concave lanceolate plate, carinate, with long free blade; aboral pit near center.

(New definition.) A representative of Polygnathidae with large free blade, ±arched and sculptured plate which always meets the B-ward tip. Rim of plate in most cases somewhat higher than its portion near the carina which is subcentral and may or may not reach the B-ward tip. Ordinarily no secondary carinae are developed. An escutcheon is present, the keel is uninterrupted on both sides of it and meets the B-ward tip. No secondary keels are present on normal specimens. The crimp is more or less broad.

*Recorded range.*—Lower Devonian-Upper Mississippian. (*Polygnathus mungoensis* most probably belongs to another genus.)




TEXT-FIG. 4—Morphology of *Polygnathus*.

### POLYGNATHUS AMANA Müller & Müller, n. sp.
Pl. 135, fig. 4

*Polygnathus* n. sp. MEHL & QUIGLEY *in* Branson, 1944, Mo. Univ. Stud., vol. 19, no. 3, p. 156, pl. 27, fig. 5, [After C. M. Quigley's master's thesis (1942)].

*Holotype.*—Original of Pl. 135, fig. 4.

*Locus typicus and stratum typicum.*—Amana beds at State Highway 220 near Middle Amana, layer 11.

*Derivatio nominis.*—After the type locality.

*Diagnosis.*—A representative of *Polygnathus* with a long free blade and narrow, elongate, strongly bowed plate. The sculpture consists of transverse ridges. Escutcheon small, crimp broad.

*Description.*—Free blade long and straight, highest point is near the A-end. Slant steep bearing only one denticle. Denticles regular in size, elongate, and discrete. Carina distinct; its denticles become more prominent in the middle of the unit, and taper out toward the B-tip of plate. The

carina is strongly bowed (convex toward C). Plate strongly arched and narrow, greatest width is near or just B-ward of their middle. Rim on C-side begins with a sharp angle, and has a distinct sinus in the A-portion. Further, it is convex but may have a shallow indentation near the sharply pointed B-tip. The D-rim is nearly straight and may have a shallow sinus near the A-ward limit of plate. The sculpture of the plate is composed of ridges of fused nodes, normal to the rim. On the A-side of plate distinct troughs are developed, in this portion the rims are much higher than the middle of plate near carina.

Lower side: keel well developed, highest at the tips, but always connected in the middle. Escutcheon oval and small, its position is in the A-ward third of the plate. The crimp is broad.

*Comparison.*—On the similar *Polygnathus webbi* Stauffer, 1938, which is present in the Sweetland Creek shale, the plate is not as strongly arched, the sculpture is coarser and the ridges are arranged in a fan-like fashion; furthermore the carina is distinct on the B-tip.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 5,9–11, and westernmost outcrop beneath the Pennsylvanian sandstone. Independence shale at the county farm near Independence, outcrop at the crossroad and in the creek bed. North Liberty beds 1½ miles northeast of North Liberty. Sylamore sandstone in Missouri.

*Types.*—Holotype SUI 9915; unfigured paratypes SUI 9916.

### POLYGNATHUS FOLIATA Bryant
### Pl. 135, fig. 1

*Polygnathus foliatus* BRYANT, 1921, Buff. Soc. Nat. Science Bull., vol. 13, p. 24, pl. 10, fig. 13–16.

v. *Polygnathus delicatulus* ULRICH & BASSLER, 1926, U. S. Nat. Mus. Proc., vol. 68, art. 12, p. 45, pl. 7, fig. 9,10? [9 = lectotype designated here].

*Polygnathus foliatus* HOLMES, 1928, U. S. Nat. Mus. Proc., vol. 72, art. 5, p. 17.

*Polygnathus angusta* BRANSON & MEHL, 1934, Mo. Univ. Stud., vol. 8, p. 245, pl. 20, fig. 14 [*cet. excl.*]

*Polygnathus foliata* HUDDLE, 1934, Bull. Amer. Paleont., vol. 21, no. 72, p. 99, pl. 8, fig. 14,15 [non. 16–17 = *P. normalis*].

*Polygnathus decorosus* STAUFFER, 1938, Jour. Paleont., vol. 12, p. 438, pl. 53, fig. 1,5,6,10,11, 15,16,20,30.

*Polygnathus xylus* STAUFFER, 1940, Jour. Paleont., vol. 14, p. 430, pl. 60, fig. 42,50,54, 65–67,69,72–74. [non. 78–79].

?*Polygnathus foliata* MEHL & QUIGLEY *in* Branson, 1944, Mo. Univ. Stud., vol. 19, no. 3, p. 158, pl. 27, fig. 1–3. [non 4].

v. *Polygnathus decorosa* YOUNGQUIST, 1947, Jour. Paleont., vol. 21, p. 109, pl. 24, fig. 21.

v. *Polygnathus parviuscula* YOUNGQUIST, 1947, ibid., p. 109, pl. 25, fig. 8,13,16, [= small growth stages].

v. non! *Polygnathus decorosa* YOUNGQUIST & PETERSON, 1947, ibid., p. 250, pl. 36, fig. 10–12, [= *Ctenopolygnathus* sp.].

v. *Polygnathus decorosa* MILLER & YOUNGQUIST, 1947, ibid., p. 514, pl. 74, fig. 6,7.

v. *Polygnathus longipostica* YOUNGQUIST & MILLER, 1948, ibid., vol. 22, p. 448, pl. 68, fig. 12.

v. *Polygnathus* sp. YOUNGQUIST & MILLER, 1948, ibid., p. 449, pl. 68, fig. 9.

*Polygnathus decorosa* BISCHOFF, 1956, Notizbl. Hessisches L.-Amt Bodenforschung, vol. 84, p. 132, pl. 9, fig. 15–17,20,23.

*Diagnosis.*—A representative of *Polygnathus* with a long free blade with regular

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### EXPLANATION OF PLATE 137

All specimens are from the Amana beds at State Highway 220 near Middle Amana, Iowa Co., Iowa. All figures are unretouched photographs, ×40.

FIG. *1,2*—*Ancyropenta longidenticulata*, n. sp. *1*, holotype, sinistral; *a*, upper view; *b*, lateral view (from C). Layer 7. *2*, sinistral specimen, lower view, demonstrates the increasing toward the rim of the B-ward secondary keel, the escutcheon is concealed by remnants of the base. Layer 7. (See also Pl. 136, fig. 3.)

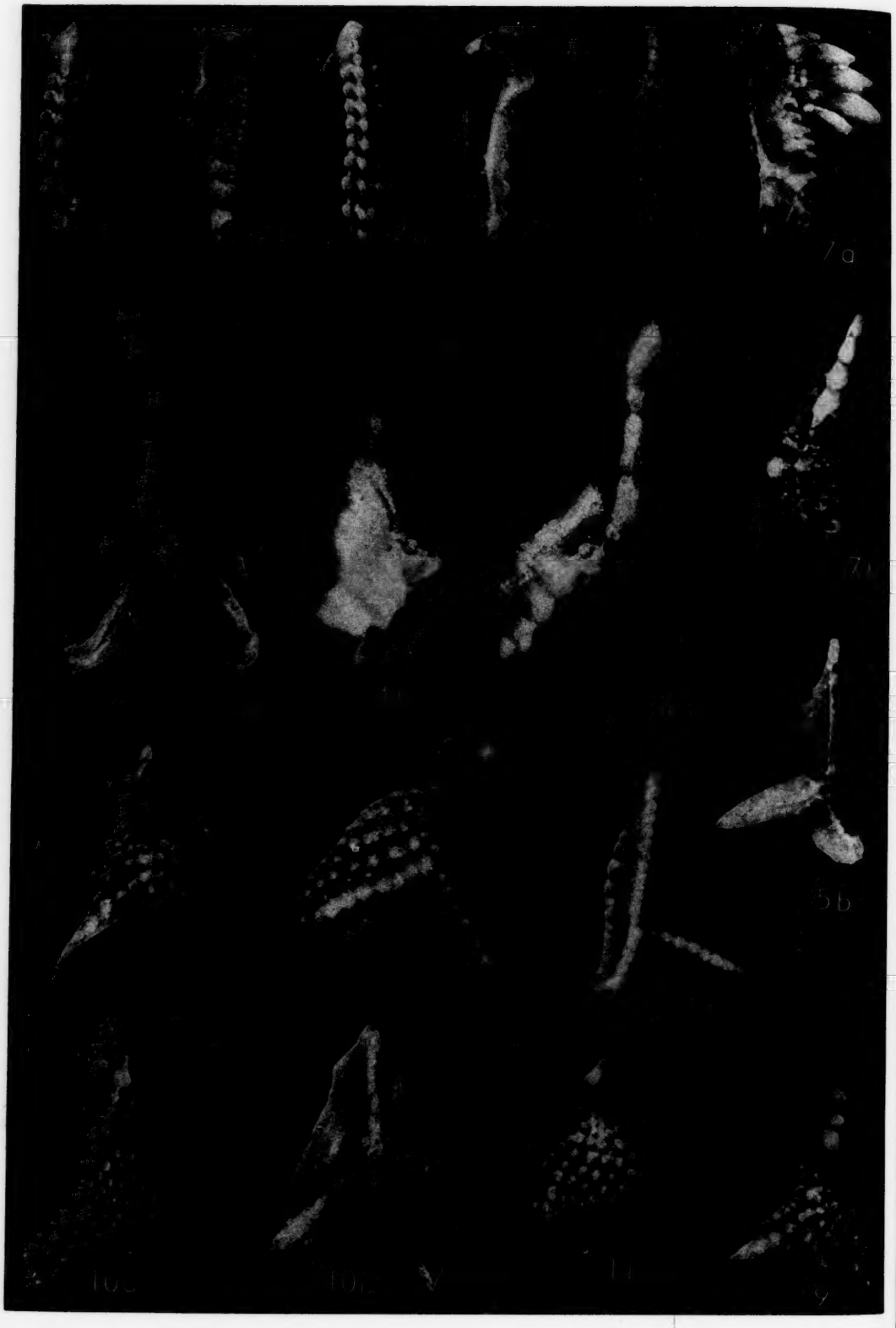
*3,6*—*Ancyrognathus triangularis* Youngquist. *3*, small, sinistral specimen. Layer 5. *6*, large, sinistral specimen, demonstrates the increased growth of the A-ward portion; *a*, upper view; *b*, lateral view (from C). Layer 7.

*4*—*Ancyrognathus?* sp. *B*. Fragment of large sinistral specimen. Layer 3.

*5*—*Ancyrognathus iowaensis* Youngquist, Sinistral, large specimen; the blade has a somewhat oblique position (pathologic?). Layer 7.

*7*—*Ancyroides princeps* Miller & Youngquist. Fragment of dextral specimen. Layer 8.

1a
1b
2
3
4
7
5
6
a
b



denticles and a distinct, bowed carina which meets the B-ward tip. Plate narrow, elongate, rims are higher than the portion of plate near the carina. Plate adorned with nodes or ridges normal to the rim. A small escutcheon is developed in the A-ward third of plate, the crimp is broad.

*Description.*—Free blade fairly high, very long and straight, highest point only little higher than the remainder, in or just behind its A-ward third. Denticles regular, large, long, and fused with exception of the tips. Slant fairly steep and denticulate. Carina distinct, bowed (convex toward C); its denticles are more or less fused. Toward B it decreases little in height, and in most cases it meets the tip. Plate strongly arched, narrow and elongate; rim on C-side ±regularly convex, on D-side less convex or straight. B-ward tip pointed ±blunt. The rim is much higher than the portion of plate beside the carina. The sculpture of plate consists of irregular nodes, in some cases arranged in ridges normal to the rim. Lower side: keel prominent, escutcheon small, elongate and in the first third of plate. The crimp is broad.

*Remarks.*—The identity of this species has been proved by comparison with material from Bryant's type locality. *P. multinodosa* is regarded as only a variety of this species with somewhat enlarged width of plate. The specimens of Mehl & Quigley from the Sylamore seem to demonstrate this same tendency.

*P. procera* Sannemann, 1955, is similar, but has a tapering slant which is denticulate in a fan-like fashion. *P. longipostica* Branson & Mehl, 1934, is to distinguish from this species by the lack of a regular bowing of carina, which is nearly straight and increases in height toward both ends; furthermore the escutcheon is much larger.

*Range.*—The species may prove to be restricted to the Frasnian; it is recorded from the lowermost as well as the upper part.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 1–3,5–13, and westernmost outcrop beneath the Pennsylvanian sandstone. Independence shale at the county farm near Independence, outcrops at the crossroad and in the creek bed. Limestone bed in Independence shale at Brandon. Independence shale in Benton County, Sec. 9, T86N, R6W. Sweetland Creek shale near Muscatine; lower, middle, upper layer at Campbell's Run; undifferentiated in other outcrops. Filling of a sinkhole in Cedar Valley limestone at Solon. North Liberty beds 1½ miles northeast of North Liberty.

Genundewa limestone, New York; Hardin sandstone, Tennessee; Grassy Creek shale, Missouri; lower New Albany shale, Indiana; Olentangy shale, Ohio; Widder beds, Ontario; upper part of Cedar Valley limestone and clay above Cedar Valley limestone, Minnesota; Sylamore sandstone, Missouri?

Kellwasserkalk, West Germany.—Widespread and common.

*Figured specimen.*—SUI 9912.

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EXPLANATION OF PLATE 138

All specimens are from the Amana beds at State Highway 220 near Middle Amana, Iowa Co., Iowa. All figures are unretouched photographs, ×40.

FIG. *1–3*—*Icriodus symmetricus* Branson & Mehl. *1*, dextral specimen. Layer 8. *2*, sinistral specimen; *a*, upper view; *b*, lateral view (from D); *c*, lower view. Layer 8. *3*, dextral specimen. Layer 8. (See also Pl. 8, fig. 142.)

*4*—*Ancyrognathus alta*, n. sp. Holotype, dextral; *a*, upper view; *b*, lateral view (from C); *c*, lower view, demonstrates the broad crimp. Layer 8. (Comp. with Pl. 141, fig. 5.)

*5*—*Ancyrognathus amana*, n. sp. Holotype, sinistral; *a*, upper view; *b*, lower view. Layer 7.

*6*—*Ancyroides calvini* Miller & Youngquist. Sinistral specimen. Layer 11.

*7*—*Ancyroides euglypheus* (Stauffer). Dextral specimen; *a*, lateral view (from C); *b*, upper view. Layer 8.

*8,9*—*Ancyroides asymmetrica* (Ulrich & Bassler). *8*, dextral specimen. Layer 11. *9*, dextral specimen. Layer 11. (See also Pl. 141, fig. 4,6,7.)

*10,11*—*Ancyroides uddeni* Miller & Youngquist. *10*, sinistral specimen; *a*, upper view, the change in course of C-rim during ontogeny is visible in the arrangement of nodes; *b*, lower view. Layer 11. *11*, dextral specimen. Layer 11.

### POLYGNATHUS GRANULOSA
Branson & Mehl
Pl. 135, fig. 2,8; Pl. 141, fig. 1

*Polygnathus granulosa* BRANSON & MEHL, 1934, Mo. Univ. Stud., vol. 8, p. 246, pl. 20, fig. 21,23.

non! *Polygnathus granulosa* THOMAS, 1949, Geol. Soc. Amer. Bull., vol. 60, p. 408, pl. 1, fig. 33, 34.

v. *Polygnathus brevis* MILLER & YOUNGQUIST, 1947, Jour. Paleont., vol. 21, p. 514, pl. 74, fig. 9.

v. *Polygnathus*? *rugicosta* MILLER & YOUNGQUIST, 1947, ibid., p. 515, pl. 74, fig. 15. [large fragment of gerontic specimen].

*Diagnosis.*—A representative of *Polygnathus* with a short, stout blade. The carina is considerably bowed. The plate is strongly arched, broad, and sculptured, and has pronounced troughs on the A-ward half. The escutcheon is small, the crimp broad.

*Description.*—Blade short, stout and fairly high; growth lines in the blade are fanlike arranged on many specimens, with the center at the A-ward tip of plate. Slant steep, in many cases (Pl. 135, fig. 2b) bearing a number of small denticles. Denticles of blade large, irregular and fused with exception of tips. Carina strongly bowed, convex toward C, and increasing in width, but decreasing in height toward the center of unit. It tapers toward the B-tip which may or may not be met.

Plate strongly arched, broad, rim on both sides of the blade beginning with a sharp process, and ±convex with few shallow indentations up to the pointed B-tip. On some, particularly larger specimens the rim on D-side is concave. At least on larger specimens B-tip is the most D-ward point of the unit. Sculpture consisting of nodes or irregular ridges, somewhat coarser on the A-ward half than on the B-portion. Lower side has a strongly developed and uninterrupted keel and a small oval-triangular escutcheon in the A-ward first quarter of plate. The crimp is broad.

*Remarks.*—Specimens from Amana are in good agreement with the original descriptions of Branson & Mehl. Slight differences in the pattern of sculpture, which consist of irregular nodes on the holotype, are referred to ontogenetic development; the holotype being only about 0.7 mm. long, compared with 1.3 mm. of the smallest specimen figured here (Pl. 135, fig. 2). In bowing of the B-ward portion of plate toward D mature specimens (comp. Pl. 135, fig. 8a,b) demonstrate a tendency similar to the general pattern of *P. linguiformis* Hinde, 1879. There seems to be no closer relationship between these species.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 2,5–8. Independence shale at the county farm near Independence, outcrops at the crossroad and in the creek bed. Sweetland Creek shale near Muscatine; undifferentiated. Grassy Creek shale, Missouri.

*Figured specimens.*—SUI 9913, SUI 9921, SUI 9964.

### POLYGNATHUS INDEPENDENSIS
Müller & Müller, n. sp.
Pl. 141, fig. 2,9

*Holotype.*—Original of Pl. 141, fig. 2

*Locus typicus and stratum typicum.*—Independence beds at the county farm near Independence, Buchanan County, Iowa. Outcrop in the creek bed.

*Derivatio nominis.*—After the *locus typicus.*

*Diagnosis.*—A representative of *Polygnathus* with fairly large free blade and slightly arched plate which is narrow in A-portion and becomes conspicuously biconvex toward its middle. Carina slightly bowed, does not meet the B-tip. Escutcheon in A-ward quarter of plate; the crimp is fairly broad.

*Description.*—Blade fairly large, its denticles are elongate and irregular, slant denticulate and relatively flat. Carina narrow at the blade, increasing considerably in width toward the middle of plate, then thinning out toward the B-tip which is not met. Plate little arched, narrow on the A-side, and wide in the middle, narrowing B-ward from its middle. Characteristically there is a waistlike narrowing behind about the first quarter of plate. B-tip in most cases pointed, in a few specimens (*e.g.*, Pl. 141, fig. 9) rounded. Sculpture consists of rows of irregular nodes, perpendicular to the rim. Troughs are distinguishable on more than the A-ward half of plate. Escutcheon oval and elongate in first quarter of plate. Crimp fairly broad, but narrower than in *P. foliata.*

*Remarks.*—This species is similar to *P.*

*amana* in blade, carina, and particularly development of a "waist." Outline, degree of arching of plate, and pattern of sculpture, however, are clearly distinct.

*Occurrence.*—Independence shale at the county farm near Independence, outcrop in the creek bed. Sweetland Creek shale near Muscatine, upper layer at Campbell's Run. Amana beds at State Highway 220 near Middle Amana, layer 9.

*Types.*—Holotype SUI 9965; figured paratype SUI 9972; unfigured paratypes SUI 9973.

### POLYGNATHUS NORMALIS
Miller & Youngquist
Pl. 135, fig. 9; Pl. 141, fig. 3

*Polygnathus foliata* HUDDLE, 1934, Bull. Amer. Paleont., vol. 21, no. 72, p. 99, pl. 8, fig. 16,17. [non 14,15 = *P. foliata*].

v. *Polygnathus normalis* MILLER & YOUNGQUIST, 1947, Jour. Paleont., vol. 21, p. 515, pl. 74, fig. 4,5.

*Polygnathus normalis* YOUNGQUIST & MILLER, 1948, ibid., vol. 22, p. 448, pl. 68, fig. 11. [type missing].

*Polygnathus normalis* BISCHOFF, 1956, Notizbl. Hessisches L.-Amt Bodenforschung, vol. 84, p. 133, pl. 9, fig. 18.

*Diagnosis.*—A representative of *Polygnathus* with fairly large free blade. Carina bowed, does generally not meet the B-tip. The escutcheon is small and subcentral, the crimp is broad.

*Description.*—Blade fairly large, its denticles are small and regular. Slant rounded. Carina distinct, regularly bowed (convex toward C). Increases in width B-ward of center of plate, then decreases again and does not meet the B-tip. Plate slightly arched, fairly broad and increasing in width toward the center of unit. C-rim rounded, D-rim nearly straight, plate on C-side thus more developed than on D-side. B-tip blunt, forming the deepest portion of plate.

The rims are much higher than the portion near the carina, particularly in the A-ward half of plate. Sculpture consists of subregular ridges perpendicular, slightly fanlike, to the rim. It is best developed near the rim and becomes obsolete toward the carina. Troughs are developed on both sides of carina at least on the A-ward half of plate.

Lower side: keel prominent, escutcheon behind the A-ward third of plate and small, crimp broad.

*Remarks.*—This species is close to *P. foliata* from which it may have originated by enlargement of the plate and reduction of the carina in the B-portion.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 8–10, ?13, and westernmost outcrop beneath the Pennsylvanian sandstone. Independence shale at the county farm near Independence, outcrops at the crossroad and in the creek bed. Independence shale in Benton County, sec. 9, T86N, R6W. North Liberty beds 1½ miles northeast of North Liberty. Sweetland Creek shale: Lower New Albany shale, Indiana: Kellwasserkalk, West Germany.

*Figured specimens.*—SUI 9922, SUI 9966.

### POLYGNATHUS UNICORNIS
Müller & Müller, n. sp.
Pl. 135, fig. 5–7; Pl. 141, fig. 10

*Holotype.*—Original of Pl. 135, fig. 5a–c.

*Locus typicus and stratum typicum.*—Amana beds at State Highway 220 near Middle Amana, layer 6.

*Derivatio nominis.*—Because of the hornlike large denticle on the blade.

*Diagnosis.*—A representative of *Polygnathus* with a short stout blade, which bears only 1–4 extremely large and irregular denticles and a broad but shallow carina which meets the B-ward tip of plate. Plate narrow, arched but little bowed. The small escutcheon is triangular, the crimp fairly narrow.

*Description.*—Free blade relatively short and stout, the highest point is on the A-end. Slant steep and undenticulate. The blade has only one or a few high and large denticles which decrease ±abruptly toward the shallow and broad carina. Denticles on carina fused and indistinct. Carina always meets the B-tip.

Plate strongly arched, narrow, straight or nearly straight. Both rims are slightly convex and without sinus. They are higher than the portion of plate adjacent to the carina. Troughs well developed, deepest on A-side, but visible on about two-thirds of plate. Sculpture consists of irregular nodes, which decrease in size toward the rim. Keel well developed, highest on the tips, but always uninterrupted. Escutcheon in the A-ward quarter of plate, fairly large. It forms a triangle, the smaller side of which is directed

toward A, while a corner points toward B. However, this feature does not seem to be very constant, and in some cases the escutcheon is drop-shaped, the broader part being on the A-side. The crimp is fairly narrow. Keel beneath the blade convex, the lower limit thus forming a slight S (Pl. 135, fig. 5b).

*Remarks.*—This species possibly has originated from a form like *P. foliata*. The narrow and strongly arched plate, and the long carina are regarded as primitive features, while the short and stout blade with only a few denticles is highly specialized.

About 5% of the specimens available for study have a secondary keel (comp. Pl. 135, fig. 6) or secondary carina (comp. Pl. 141, fig. 10). Their position is different on every specimen. Therefore, we do not regard these features as significant for taxonomy, but with some reservation as instability in development, inherent in this species. If such features would be constant in species, these would have to be excluded from *Polygnathus* and assigned to *Ancyrognathus*.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 1–3,5–8, and westernmost outcrop beneath the Pennsylvanian sandstone. Independence shale at the county farm near Independence, outcrops at the crossroad and in the creek bed. Limestone bed in Independence shale at Brandon. Sweetland Creek shale near Muscatine, middle and upper layer at Campbell's Run. North Liberty beds 1½ miles northeast of North Liberty.

*Types.*—Holotype SUI 9917; figured atypical sepcimens SUI 9918, SUI 9919, SUI 9974; unfigured typical specimens SUI 9920.

### Ancyro Group

Genera which have names beginning with *Ancyro-* have produced many large and conspicuous forms, and many excellent index fossils in early Upper Devonian. These forms have strongly developed secondary keels and the upper surface of the plate is adorned with a prominent sculpture. The genera have originated from *Polygnathus* independently, with the exception of *Ancyropenta* which developed from *Ancyrognathus*. Although these forms have a certain similarity it seems inadvisable to establish a taxon for the unit, but a determination key may be useful.

ARTIFICIAL KEY FOR THE ANCYRO GROUP

1. With two secondary keels on A-portion.....4
2. Without secondary keels on A-portion.....3
3. With one secondary keel on B-portion
   a. Blade short and high, toward B ending abruptly.....*Ancyroides*
   b. Blade tapers toward a carina.....*Ancyrognathus*
4. With two secondary keels, directed toward A
   a. No secondary keel on the B-side.....*Ancyrodella*
   b. One secondary keel on the B-side.....*Ancyropenta*

### Genus Ancyrodella Ulrich & Bassler, 1926

*Type species.*—*Ancyrodella nodosa* Ulrich & Bassler, 1926.

*Diagnosis.*—(New definition.) A representative of Polygnathidae with large more or less arched and sculptured plate, a quite prominent blade (on A-side), and with two subsymmetric secondary carinae which are directed toward A. Carina slightly bowed (convex toward C) or straight, reaches the B-ward tip which is arched downward and forms the deepest point of the plate. Plate trilobate and in most cases sculptured by nodes or ridges. The lower side has a well developed escutcheon beneath the growth center which is larger than in most other genera of Polygnathidae. Keel and secondary keels which meet at the escutcheon are developed beneath the carina and lateral carinae.

*Occurrence.*—The genus seems to be restricted to the early Upper Devonian. It is common and widely distributed in America, Europe and Australia. Species of this genus are regarded to be excellent index fossils.

*Remarks.*—The occurrences of *Ancyrodella* in the Hardin sandstone at Mt. Pleasant, Tennessee (Ulrich & Bassler, 1926) and in the Saverton of Missouri are regarded as secondary deposits.

The following features in various combinations are regarded as useful for recognition of species: degree of symmetry of the unit; outline, particularly shape of B-end; sculpture, particularly differences in shape and relative size of nodes; angle between secondary keels; width of the crimp; size

and shape of escutcheon; size and pattern of denticulation of blade; presence and size of trough.

### ANCYRODELLA BUCKEYENSIS Stauffer
Pl. 136, fig. 5,?2

*Ancyrodella buckeyensis* STAUFFER, 1938, Jour. Paleont., vol. 12, p. 418, pl. 52, fig. 17,18,23,24. [23 = lectotype designated here].
v. *Ancyrodella buckeyensis* YOUNGQUIST, 1945, ibid., vol. 19, p. 356, pl. 54, fig. 11.
v. *Polygnathus rotundiloba* YOUNGQUIST, 1947, ibid., vol. 21, p. 110, pl. 26, fig. 6.
v. *Polygnathus spinulosa* YOUNGQUIST, 1947, ibid., vol. 21, p. 110, pl. 24, fig. 9.
v. *Ancyrodella* sp. MILLER & YOUNGQUIST, 1947, ibid., vol. 21, p. 503, pl. 74, fig. 13.
v. *Ancyrodella lobata* MILLER & YOUNGQUIST, 1947, ibid., vol. 21, p. 502, pl. 74, fig. 12. [non 10 = *subrotunda*, 11 = *hamata*].
v. *Ancyrodella nodosa* YOUNGQUIST & MILLER, 1948, ibid., vol. 22, p. 441, pl. 68, fig. 14,13.

*Diagnosis.*—A subsymmetrical representative of *Ancyrodella* with regularly shaped outline and sculpture, consisting of ridges normal to the rim.

*Description.*—Blade and carina are straight or nearly straight, only little arched, denticles on both regular and small. Outline of plate triangular, B-end is regularly pointed. Secondary carinae relatively fine; the first denticle from the blade on C-side has an odd position toward B. Sculpture on upper side of plate consists of fairly regular small ridges, standing normal to the rim. The secondary keel angle is about 90°, the crimp is broad, the escutcheon well developed.

The specimen figured on Pl. 136, fig. 2, probably is only a more mature specimen of this species. The carina is still straight in general direction but slightly sigmoidal and the B-tip more pointed than on smaller specimens. The conspicuous pattern of sculpture and the width of crimp corresponds to *A. buckeyensis*.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 7,8,?10,11,13. Independence shale at the county farm near Independence, outcrops at crossroad, and in the creek bed. Sweetland Creek shale near Muscatine, upper layer at Campbell's Run, and undifferentiated in other outcrops. Filling of a sinkhole in Cedar Valley limestone at Solon. North Liberty beds 1½ miles northeast of North Liberty. Originally described from the Olentangy shale, Ohio.

*Figured specimens.*—SUI 9926, SUI 8079.

### ANCYRODELLA GIGAS Youngquist
Pl. 141, fig. 8; Pl. 142, fig. 1

v. *Ancyrodella gigas* YOUNGQUIST, 1947, Jour. Paleont., vol. 21, p. 96, pl. 25, fig. 23.
v. *Ancyrodella magister* MILLER & YOUNGQUIST, 1947, ibid., vol. 21, p. 503, pl. 74, fig. 14.

*Diagnosis.*—A representative of *Ancyrodella* with a pointed B-end and a fine, distinct tuberculation on the upper surface of plate. The crimp is narrow.

*Description.*—Blade and carina slightly bowed (convex toward C). Axis little arched. Denticles on blade large, irregular, discrete and sphene-shaped. The largest ones are near the A-end.

Denticles on carina ±rounded in cross section and discrete. Carina meets the B-tip. Secondary carinae regular and subsymmetrical, not very prominent. Sculpture on the upper side of plate consists of numerous irregularly arranged, distinct, rounded, small nodes. Secondary keel angle about 80–100°, becoming a little more acute toward the rim in larger specimens. The crimp is narrow, the escutcheon small.

*Remarks.*—This species is readily recognized by the fine and distinct tuberculation of plate.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 10–13. Independence shale at the county farm near Independence, outcrop in the creek bed. Sweetland creek shale near Muscatine, upper layer at Campbell's Run, and undifferentiated. North Liberty beds 1½ miles northeast of North Liberty.

*Figured specimens.*—SUI 9971, SUI 9975.

### ANCYRODELLA HAMATA Ulrich & Bassler
Pl. 136, fig. 4

v. *Ancyrodella hamata* ULRICH & BASSLER, 1926, U. S. Nat. Mus. Proc., vol. 68, p. 48, pl. 7, fig. 7.
v. *Ancyrodella symmetrica* ULRICH & BASSLER, 1926, ibid., p. 49, pl. 8, fig. 1.
*Ancyrodella hamata* BASSLER, 1932, Tenn. Div. Geol. Bull. 38, p. 234, pl. 26, fig. 14. [cf. Ulrich & Bassler, 1926, pl. 7, fig. 7].
?*Ancyrodella hamata* COOPER, 1935, Jour. Paleont., vol. 9, p. 310, pl. 27, fig. 39.
v. *Ancyrodella lobata* MILLER & YOUNGQUIST, 1947, ibid., vol. 21, p. 502, pl. 74, fig. 11. [non 10 = *subrotunda*, 12 = *buckeyensis*].

*Diagnosis.*—A prepresentative of *Ancyrodella* with bowed blade and carina, irregular outline and coarse nodes on plate which are arranged lengthwise and rounded.

*Description.*—Blade and carina bowed, convex toward C. Axis strongly arched, particularly near the B-ward tip, which is the deepest point of the plate. The blade is adorned with very large, long denticles. The carina in relatively high, the denticles are small and somewhat fused. Outline of plate irregular, B-end pointed. Secondary carinae adorned with large discrete denticles. The upper side of plate has a coarse sculpture consisting of rounded nodes which are arranged in 2–3 rows, parallel to the rim. The secondary keel angle is >50°, the crimp broad. On the figured specimen the escutcheon is small.

*Comparisons.*—Compared to *Ancyropenta lobata*, which probably has developed from this species, there is a lack of the additional B-ward secondary keel, and a somewhat more obtuse secondary keel angle.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 1–3,5–10,12, and westernmost outcrop beneath the Pennsylvanian sandstone. Independence shale at the county farm near Independence, outcrops at the crossroad and in the creek bed. Sweetland Creek shale near Muscatine, upper layer at Campbell's Run, and undifferentiated in other outcrops. North Liberty beds 1½ miles northeast of North Liberty. Hardin sandstone, Tennessee, Arkansas novaculite, Arkansas?

*Figured specimen.*—SUI 9928.

### ANCYRODELLA SUBROTUNDA Miller & Youngquist
Pl. 136, fig. 6

v. *Ancyrodella subrotunda* MILLER & YOUNGQUIST, 1947, Jour. Paleont., vol. 21, p. 503, pl. 74, fig. 17. [=holotype].
*Ancyrodella lobata* MILLER & YOUNGQUIST, 1947, ibid., p. 502, pl. 74, fig. 10. [non 11=*hamata*, 12=*buckeyensis*].

*Diagnosis.*—A subsymmetrical representative of *Ancyrodella* with rounded B-portion and shallow, irregular sculpture; the secondary keel angle is sharp.

*Description.*—Blade and carina nearly straight, only little arched. Blade adorned with large irregular denticles which are largest at the highest point of blade and become smaller toward the carina. Denticles on the carina ±fused, and on larger specimens only faint. Outline of unit may be characterized as hexagonal, B-end rounded and blunt particularly on larger specimens. Secondary carinae fairly well pronounced, their denticles may be fused. Sculpture on upper side of plate consists of shallow nodes of variable size which are equally distributed over the entire plate. Secondary keel angle about 70°. The crimp is narrow. The escutcheon on the holotype is narrow and elongate; it is invisible on the figured specimen.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 3,7, and with ? westernmost outcrop beneath the Pennsylvanian sandstone. Sweetland Creek shale near Muscatine, undifferentiated. With ? North Liberty beds 1½ miles northeast of North Liberty.

*Figured specimen.*—SUI 9929.

### Genus ANCYROPENTA Müller & Müller, n. gen.

*Type species.*—*Ancyrognathus curvata* Branson & Mehl, 1934.

*Derivatio nominis.*—Composed from *ancyro-* as in *Ancyrodella*, *Ancyrognathus*, and *Ancyroides*, and πεντα(=five).

*Diagnosis.*—A representative of Polygnathidae with a long arched plate which is strongly sculptured on its upper side. The blade is strongly developed, denticulate, and on the A-side of unit. The carina is well developed, slightly bowed, convex toward C, and meeting the rim on the tip of the B-limit. There are two subsymmetrical secondary carinae toward A, and one toward B which is less pronounced in some cases. All are in the center of lobes of the plate.

Lower side: there are two distinct, subsymmetrical secondary keels on the A-portion, and one pointing toward B, forming an irregular pentagram together with the strongly developed A- and B-parts of keel. The escutcheon is in the growth center on the intersection of keel and A-ward secondary keels. The B-ward secondary keel branches from the A-ward one on the C-side. The crimp is relatively broad.

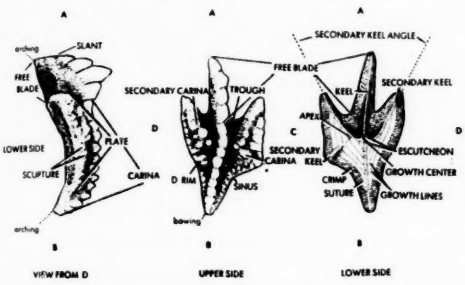
*Remarks.*—This genus has originated

from *Ancyrodella*. Transitional stages are known.

*Ancyrodella lobata* Branson & Mehl, 1934, p. 239, pl. 19, fig. 14; pl. 21, fig. 22,23 belongs to this genus in addition to the genotype and the species described below.

*Ancyropenta* has a slight resemblance to *Amorphognathus*, an Ordovician genus which has developed six or more lobes. There is no relation between these forms.

*Recorded range.*—Early Upper Devonian.




TEXT-FIG. 5—Morphology of *Ancyropenta*.

ANCYROPENTA ASTEROIDEUS (Stauffer)
Pl. 136, fig. 7a,b,8

*Ancyrognathus asteroideus* STAUFFER, 1938, Jour. Paleont., vol. 12, p. 418, pl. 52, fig. 8,9.

*Diagnosis.*—A representative of *Ancyropenta* with well developed secondary lobe toward B. The secondary carinae on B- and A-portion of unit (on C-side) form a regular bow which is separated from the carina by a trough.

*Description.*—The larger figured specimen is similar to Stauffer's type. The secondary carinae become somewhat narrower and are increasing in height toward the rim. The sculpture is composed of ridges, perpendicular to the rim. The lower side has a relatively small escutcheon and a rather broad crimp. On the small specimen (fig. 8) the D-ward deflection of keel and carina and the well developed lobe toward B are visible. At this growth stage the sculpture is not arranged in ridges.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 8.

*Figured specimens.*—SUI 9930, SUI 9931.

ANCYROPENTA LONGIDENTICULATA Müller & Müller, n. sp.
Pl. 136, fig. 3a–c; Pl. 137, fig. 1a,b,2

*Holotype.*—Original of Pl. 137, fig. 1a,b.

*Locus typicus and stratum typicum.*—Amana beds at State Highway 220 near Middle Amana, layer 7.

*Diagnosis.*—An elongate representative of *Ancyropenta* with only slightly developed secondary carina toward B, and high blade with long denticles.

*Description.*—Blade strongly developed, high and denticulate. Denticles small at the A-limit, increasing toward the greatest height, elongate, fused in the lower portion, only the tips are discrete. The maximum of height is near the center of the blade. Carina distinct, denticulate, little bowed toward D. A-ward secondary carinae distinct and subsymmetrical. Plate strongly arched, adorned with large irregular denticles. Outline has asymmetry by an additional lobe around the B-ward secondary keel. The B-ward carina is lacking in early growth stages, but distinct on larger specimens.

Lower side: keel and secondary keels toward A are well developed. B-ward secondary keel faint near the growth center and increasing in prominence toward the rim. Therefore, this feature is more distinct in gerontic than in juvenile specimens. The angle between B-portion of keel and B-ward secondary keel is about 80°. The escutcheon is small, the crimp narrow.

*Remarks.*—*Ancyropenta lobata* (Branson & Nehl, 1934) differs from this species by growth pattern of blade, stronger developed secondary keel toward B, finer, regularly arranged nodes of sculpture, and the stouter plate, as it can be observed only on rather large specimens of *A. longidenticulata*.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 2,7,8, 10–13, and westernmost outcrop beneath the Pennsylvanian sandstone. Independence shale at the county farm near Independence, outcrops at the crossroad and in the creek bed. North Liberty beds 1½ miles northeast of North Liberty.

*Types.*—Holotype SUI 9932; figured paratypes SUI 9927, SUI 9933.

Genus ANCYROGNATHUS Branson & Mehl, 1934

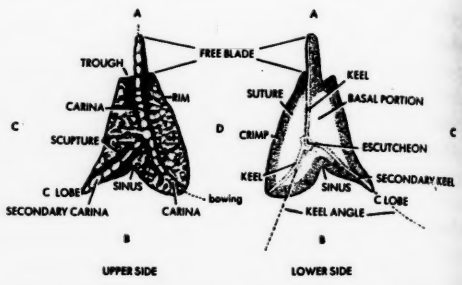
*Type species.*—*Ancyrognathus symmetrica* Branson & Mehl, 1934.

*Diagnosis.*—(After Branson & Mehl, 1934, p. 240.) Dental unit consisting of a plate nodose on the oral side and smooth on the aboral. The plate forks at the back end into two subequal lobes. A strong carina runs the length of the plate and becomes a short blade in front; at the back it forks, a branch running to the tip of each posterior lobe. Nodose ridges bisect other lobes when they are present. The aboral side of each lobe is bisected by a keel.

(New definition.) A representative of Polygnathidae with a large, irregular trifid and more or less arched plate which is often sculptured on its upper side. A strong, denticulate blade is developed on the A-side; it is continued by a generally well developed denticulate carina. A strong secondary carina branches off toward the B-ward portion of the unit, its tip directed toward B–C. The lower side shows well developed keel and secondary keel corresponding to the carina and secondary carina. Beneath the growth center an escutcheon is present which is met by the keels. The crimp is broad.

*Remarks.*—There exists a remarkable similarity with *Doliognathus* Branson & Mehl, 1941, which however has a much larger basal cavity. *Ancyrognethus quadrata* Branson & Mehl, 1934, has a large basal cavity and only one A-ward and one B-ward secondary carina; therefore, it is not regarded as belonging to any of the genera of the Ancyro-group.

*Occurrence.*—The genus seems to be restricted to the lower parts of Upper Devonian. It is common and widely distributed in North America, Europe and Australia.




TEXT-FIG. 6—Morphology of *Ancyrognathus.*

Species may be used as index fossils for subdivision in early Upper Devonian.

ANCYROGNATHUS ALTA Müller & Müller, n. sp.
Pl. 138, fig. 4a–c

*Holotype.*—Original of Pl. 138, fig. 4a–c.

*Locus typicus and stratum typicum.*—Amana beds at State Highway 220 near Middle Amana, layer 8.

*Derivatio nominis.*—Named for the extremely high carina.

*Diagnosis.*—A representative of *Ancyrognathus* with an extremely high, nearly undenticulate carina and secondary carina. The keel angle is acute, the crimp broad.

*Description.*—Blade high, long and thick at its lower limit, forming on the A-end a steep, very long and undenticulate slant. Denticles entirely fused to an irregular ridge. Carina almost as high as blade, and little bowed toward D. Plate nearly straight, meeting the tip on A-side, narrow and unsculptured. Secondary carina well developed, decreasing in height toward the tip. The keels are distinct, the keel angle is

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EXPLANATION OF PLATE 139

All specimens are from the Amana beds at State Highway 220 near Middle Amana, Iowa Co., Iowa. All figures are unretouched photographs, ×40.

FIG. *1*—*Palmatolepis* (*Manticolepis*) *subrecta* (Miller & Youngquist). Sinistral specimen; *a*, upper view; *b*, lower view, demonstrates strongly sigmoidal keel, secondary keel, and crimp. Layer 11.

*2*—*Palmatolepis* (*Manticolepis*) *hassi*, n. sp. Paratype, sinistral, small specimen. Layer 7. (See also Pl. 140, fig. 2,4.)

*3–6*—*Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer). *3*, sinistral specimen; *a*, upper view; *b*, lateral view (from C); *c*, lower view with large part of the base. Layer 7. *4*, sinistral specimen, lateral view (from C). Layer 7. *5*, sinistral specimen; *a*, upper view; *b*, lower view, demonstrates a small escutcheon. Layer 7. *6*, dextral, large specimen with gerontic development of denticles and sculpture. Layer 11. (Comp. with Pl. 142, fig. 9.)

1a
1b
2
3b
3c
3a
4
5a
5b
6a
6b

1
2
9
3
4

acute, about 80°. The crimp is rather broad.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 8.

*Holotype.*—SUI 9942.

ANCYROGNATHUS aff. A. ALTA, n. sp.
Pl. 141, fig. 5

A single specimen from Independence is similar to *A. alta* in the extreme height of carina and secondary carina which are irregularly denticulate. Furthermore, the upper surface of the plate is unsculptured. Differences are the more obtuse keel angle of about 100° and the crimp which is somewhat narrower.

*Occurrence.*—Independence shale at the county farm near Independence, outcrop in the creek bed.

*Figured specimen.*—SUI 9968.

ANCYROGNATHUS AMANA Müller & Müller, n. sp.
Pl. 138, fig. 5a,b

*Ancyrognathus* sp. A. HASS, 1956, U. S. Geol. Surv. Prof. Paper, vol. 286, tab. 7,8, pl. 4, fig. 1.

*Holotype.*—Original of Pl. 138, fig. 5.

*Locus typicus and stratum typicum.*—Amana beds at State Highway 220 near Middle Amana, layer 7.

*Derivatio nominis.*—After the type locality.

*Diagnosis.*—A representative of *Ancyrognathus* with a narrow, elongate plate and elongate and narrow pointed lobe on the C-side. Carina and secondary carina are regularly denticulate.

*Description.*—Blade low, regularly denticulate, little differentiated from carina which is straight up to the growth center, only B-portion is bowed toward D. There is no free blade. The well developed secondary carina stands perpendicular to carina; it is about half as long as carina, straight and regularly denticulate. The denticles near the growth center are somewhat smaller than the ones at the rim. Plate elongate and narrow, strongly arched. The C-lobe is also narrow, elongate and pointed. Sculpture on upper side of plate consists of a few irregular large but not high nodes near the rim, troughs are wide and developed at least up to the growth center. The keels are distinct, the keel angle is little more than 90°. The escutcheon is rather well developed at the apex. The crimp is fairly broad.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 7,8,11. Gassaway and Dowelltown members of Chattanooga shale, Tennessee.

*Types.*—Holotype SUI 9943; unfigured paratypes SUI 9944.

ANCYROGNATHUS BIFURCATA (Ulrich & Bassler)
Pl. 142, fig. 5,?11

v. *Palmatolepis bifurcata* ULRICH & BASSLER, 1926, U. S. Nat. Mus. Proc., vol. 68, art. 12, p. 50, pl. 7, fig. 16,17. [17 = lectotype designated here].

*Palmatolepis inequalis* HOLMES *in* Butts, 1926, Alabama Geol. Surv. Spec. Rep. 14, p. 160, pl. 48, fig. 7.

v. *Palmatolepis inequalis* HOLMES, 1928, U. S. Nat. Mus. Proc., vol. 72, art. 5, p. 33, pl. 11, fig. 8–10.

*Pelmatolepis bifurcatus* BASSLER, 1932, Tenn. Div. Geol. Bull., 38, pl. 26, fig. 16,17.

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EXPLANATION OF PLATE 140

All specimens are from the Amana beds at State Highway 220 near Middle Amana, Iowa Co., Iowa. All figures are unretouched photographs, ×40.

FIG. *1*—*Palmatolepis* (*Manticolepis*) *unicornis* (Miller & Youngquist). Sinistral specimen; the upper portion of the blade is not preserved. Layer 6.

*2–4*—*Palmatolepis* (*Manticolepis*) *hassi*, n. sp. *2*, dextral specimen; *a*, upper view; *b*, lateral view (from C). Layer 6. *3*, dextral specimen. Layer 8. *4*, holotype, sinistral; *a*, upper view; *b*, lateral view (from *C*); *c*, lower view, demonstrates sigmoidal keel with small escutcheon, secondary keel, and crimp. Layer 7.

*5*—*Palmatolepis* (*Manticolepis*) *amana*, n. sp. Holotype, sinistral; *a*, upper view; *b*, lateral view (from C). Layer 7.

*6–9*—*Palmatolepis* (*Manticolepis*) *foliacea* (Youngquist). *6*, dextral, small specimen. Layer 7. *7*, sinistral, small specimen. Layer 7. *8*, sinistral, mature specimen; *a*, upper view; *b*, lateral view (from C). Layer 7. *9*, dextral specimen. Layer 6.

*Ancyrognathus irregularis* BRANSON & MEHL, 1934, Mo. Univ. Stud., vol. 8, p. 242, pl. 19, fig. 4,16. [non! 1,2,10].
*Palmatolepis? inequalis* HUDDLE, 1934, Bull. Amer. Paleont., vol. 21, no. 72, p. 108, pl. 9, fig. 15–18.
?*Ancyrognathus symmetrica* MEHL & QUIGLEY in Branson, 1944, Mo. Univ. Stud., vol. 19, no. 3, p. 153, pl. 26, fig. 32. (*cet. ex.*)
*Ancyrognathus irregularis* BOND, 1947, Ohio Jour. Sci., vol. 47, p. 26, pl. 2, fig. 26.
*Ancyrognathus bifurcata* HASS, 1956, U. S. Geol. Surv. Prof. Paper, vol. 286, tab. 8, pl. 3, fig. 25,26.
?*Ancyrognathus inequalis* BISCHOFF, 1956, Notizbl. Hessisches L.-Amt Bodenf., vol. 84, p. 121, pl. 8, fig. 16.
non! v. *Ancyrognathus irregularis* YOUNGQUIST, 1947, Jour. Paleont., vol. 21, p. 97, pl. 25, fig. 21 [=*A. triangularis*].
non! *Ancyrognathus irregularis* THOMAS, 1949, Geol. Soc. Amer. Bull., vol. 60, p. 408, pl. 1, fig. 11. [=possibly close to *Polygnathus unicornis* n. sp.].

*Diagnosis.*—A representative of *Ancyrognathus* with an acute keel angle and a sculpture consisting of irregular nodes. The crimp is narrow.

*Description.*—Blade short and not very high, slant denticulate. Denticles on blade distinct and elongate, on carina often somewhat fused. Carina straight or little bowed (convex toward C), it meets the B-ward tip. Secondary carina distinct, increasing in height toward the rim. Plate fairly arched, the sculpture consists of irregular nodes which in many cases are elongate, perpendicular to the rim. Lower side shows distinct keel and secondary keel which meet at the small escutcheon in the growth center. The keel angle is acute, about 55–80°. The crimp is narrow.

*Remarks.*—The holotype of *A. bifurcata* is a large fragment and shows an acute keel angle. The sculpture resembles closely that of the specimen figured on Pl. 142, fig. 5, but is somewhat coarser, typical for a more gerontic growth stage.

Differences from *A. triangularis* are mainly the more acute keel angle, and the narrower crimp.

The cotypes of *Ancyrognathus irregularis* are not regarded as belonging to one species. According to the legend of Pl. 19 of Branson & Mehl, 1934, the type illustrated as fig. 4 is designated by these authors as an average specimen, and is selected here as lectotype. In this more restricted sense the species has an acute keel angle, compared with the obtuse or rectangular one of *A. triangularis* (Pl. 19, fig. 2,1?,10?) and thus is a junior synonym of *Ancyrognathus bifurcata* (Ulrich & Bassler, 1926).

*Occurrence.*—Sweetland Creek shale near Muscatine, lower layer at Campbell's Run. North Liberty beds 1½ miles northeast of North Liberty. Hardin sandstone, Tennessee; Chattanooga shale, Alabama; Grassy Creek shale, Missouri; Middle New Albany shale, Indiana; Sylamore sandstone, Missouri?; Ohio shale, Ohio; Gassaway and Dowelltown members of Chattanooga shale, Tennessee; Kellwasserkalk, Rhineland, Germany.

*Figured specimen.*—SUI 9979, SUI 9984.

### ANCYROGNATHUS IOWAENSIS Youngquist
Pl. 137, fig. 5

v. *Ancyrognathus iowaensis* YOUNGQUIST, 1947, Jour. Paleont., vol. 21, p. 97, pl. 25, fig. 22.
v. *Ancyrognathus cava* YOUNGQUIST, 1947, ibid., vol. 21, p. 97, pl. 24, fig. 3.

*Diagnosis.*—A representative of *Ancyrognathus* with a large slender C-ward lobe. Carina and secondary carina are distinct and increase considerably toward the rim. The keel angle is obtuse, the crimp narrow.

*Description.*—Free blade on small specimens short, denticles large and discrete. The oblique position of the blade on the figured large specimen may be due to abnormal development. Two germ denticles are visible on the holotype. Plate narrow and elongate, arched. Carina distinct, denticulate, B-portion bowed toward D. The denticles of this part are increasing in height toward B. Secondary carina well developed, increasing in height considerably toward the tip of lobe which is pointed and elongate. Sculpture composed of irregular nodes or small ridges. Lower side: the keel angle is about 130°, the crimp narrow.

*Remarks.*—This species resembles *Ancyroides ornatissimus* in the expansion of both carinae toward the tips of lobes. This fact possibly may be a clue for reconstruction of an assemblage. The holotype of *Ancyrognathus cava* Youngquist is a small specimen, the C-ward lobe of which is not preserved. All features preserved indicate that this is an early growth stage of *Ancyrognathus iowaensis.*

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 7. North

Liberty beds 1½ miles northeast of North Liberty.

*Figured specimen.*—SUI 9936.

ANCYROGNATHUS TRIANGULARIS Youngquist
Pl. 137, fig. 3,6a,b

*Ancyrognathus irregularis* BRANSON & MEHL, 1934, Mo. Univ. Stud., vol. 8, p. 242, pl. 19, fig. 2,?1,?10. [non 4,16=*bifurcata*].

v. *Ancyrognathus triangularis* YOUNGQUIST, 1945, Jour. Paleont., vol. 19, p. 356, pl. 54, fig. 7. [=holotype].

v. *Ancyrognathus irregularis* YOUNGQUIST, 1947, ibid., vol. 21, p. 97, pl. 25, fig. 21.

*Diagnosis.*—A representative of *Ancyrognathus* with a low blade, and a rounded lobe toward C. The keel angle is >90°, the crimp is broad

*Description.*—Blade low, slant denticulate, slowly increasing in height from the A-ward tip toward the growth center. Small specimens have no free blade. Denticles fused with exception of the tips. Carina distinct, not much lower than the blade, slightly bowed. The fused denticles may form an irregular crest. Troughs rather well developed. Plate little arched, triangular, its lobes are rounded. Secondary carina distinct, increases somewhat in height toward the rim. Sculpture of plate consists of more or less irregular nodes and/or ridges, normal to the rim. Lower side: keels distinct, keel angle obtuse, about 90° or somewhat more. Escutcheon is on the apex very small on the holotype. The crimp is broad.

*Remarks.*—The figure of the holotype of Youngquist (Pl. 54, fig. 7), together with the figures of a smaller and a larger specimen on Pl. 3, demonstrate the ontogeny of this species. Additional, intergrading stages have been observed. An obvious difference is the nearly equal sided triangular outline of smaller specimens compared with the much more oblong A-lobe on the larger ones. The increasing in size of the denticles on a large specimen, as figured on Pl. 137, fig. 6b, is regarded as evidence that this change of shape is a result of more pronounced growth in the A-lobe during ontogeny.

Sculpture changes from ridges perpendicular to the rim on smaller specimens toward irregular nodes on the larger ones. The secondary carina on large specimens increases stronger in height toward the rim than on early growth stages. For comparison with *A. bifurcata* see under this species.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 1,2, 4–8, and westernmost outcrop beneath the Pennsylvanian sandstone. Independence shale at the county farm near Independence, outcrop in the creek bed. Sweetland Creek shale near Muscatine, lower layer at Campbell's Run. North Liberty beds 1½ miles northeast of North Liberty. Grassy Creek shale, Missouri.

*Figured specimens.*—SUI 9934, SUI 9937.

ANCYROGNATHUS sp. A
Pl. 142, fig. 10

*Ancyrognathus euglypheus* HASS, 1956, U. S. Geol. Surv. Prof. Paper, vol. 286, tab. 7,8, pl. 4, fig. 27.

A single specimen cannot be referred to any described species. It has an obtuse keel angle of about 100°. The plate is adorned with conspicuous ridges and rows of nodes, parallel to the rim. Keel angle and width of crimp are similar to *A. triangularis*, but sculpture is arranged perpendicular to the rim in this species. Furthermore, in *Ancyrognathus* sp. A the carina is much more bowed, convex toward C, than in *A. triangularis*.

*Occurrence.*—North Liberty beds 1½ miles northeast of North Liberty. Gassaway and Dowelltown members of Chattanooga shale, Tennessee.

*Figured specimen.*—SUI 9983.

ANCYROGNATHUS? sp. B
Pl. 137, fig. 4

A fragment of a large specimens cannot be referred to any described species. The carina is broad and not denticulate. Secondary carina shallow and irregular. The upper side of platform is adorned with peculiar irregular ridges which are not observed elsewhere in this genus, but are similar to those of *Polygnathus retrorsa* Youngquist & Peterson, 1947, from the Sheffield shale. The lower side has an obtuse keel angle and a very narrow crimp.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 3.

*Figured specimen.*—SUI 9935.

### Genus ANCYROIDES Miller & Youngquist, 1947

*Type species.*—*Ancyroides princeps* Miller & Youngquist, 1947.

*Diagnosis.*—(After Miller & Youngquist, 1947, p. 504.) Conodonts which consist of an asymmetrically trifid plate and a short high prominent denticulated blade. Oral surface of plate is convex and nodose. Aboral surface is concave and has a small central escutcheon at the junction of three small keels. Blade is low anteriorly but high posteriorly where it ends abruptly; it is confined to anterior lobe of plate on which it is typically not median in position.

(New definition.) A representative of Polygnathidae characteristically having an asymmetrical, trilobate, more or less arched and conspicuously sculptured plate. It has a very short and high denticulate blade which is confined to the A-lobe. The largest denticle of the blade is near its B-limit, which is abrupt. Carina and secondary carina which is in the lobe on the C-side, are little developed or lacking at all. Keel and secondary keel on the lower side are strongly developed. Beneath the growth center a small escutcheon is present. The crimp is broad.

*Remarks.*—The genus resembles superficially *Ancyrognathus* from which it may be distinguished by the abrupt B-limit of the blade. Most probably it originated independently from *Polygnathus*, as is suggested by *A. euglypheus*. Position of escutcheon is just before the apex; only on *A. euglypheus* is it right on the apex. Features regarded as criteria for distinction of species are keel angle, presence and growth pattern of carinae, outline, width of crimp, position of blade either median or marginal, and pattern of sculpture.

*Occurrence.*—The genus is widely distributed in Europe, North America and Australia, and is probably restricted to a zone in upper lower Upper Devonian.

### ANCYROIDES ASYMMETRICA (Ulrich & Bassler)

Pl. 138, fig. 8,9; Pl. 141, fig. 4,6,7.

v. *Palmatolepis asymmetrica* ULRICH & BASSLER, 1926, U. S. Nat. Mus. Proc., vol. 68, art. 12, p. 50, pl. 7, fig. 18.
v. *Ancyroides uddeni* MILLER & YOUNGQUIST, 1947, Jour. Paleont., vol. 21, p. 505, pl. 74, fig. 16. [non pl. 75, fig. 5 = *A. uddeni*].
v. ?*Ancyroides calvini* YOUNGQUIST & MILLER, 1948, ibid., vol. 22, p. 441, pl. 68, fig. 16.
v. *Ancyroides* aff. *A. uddeni* MÜLLER, 1956, ibid., vol. 30, p. 1340, pl. 145, fig. 15–18.
*Ancyrognathus euglypheus* BISCHOFF, 1956, Notizbl. Hessisches L.-Amt Bodenforsch., vol. 84, p. 120, pl. 8, fig. 1,2?,3?,4–8,14.

*Diagnosis.*—A representative of *Ancyroides* with blade in the middle of or submarginal in A-lobe, and a narrow, asymmetrical plate. Carina is little developed; secondary carina increases strongly in height toward the rim, thus being more prominent than the carina. The keel angle is less than 90° at the apex.

*Description.*—The blade is fairly short, and typically in the median line of the A-lobe. Plate elongate, sinus in B-C-rim irregular. The lobes are pointed and the one toward C is longer than the others. Sculpture of plate consists of regular, rounded nodes which are arranged lengthwise. Keel and secondary keel meet the rim in the middle of lobes. The keel angle near the apex is 90° or less. The escutcheon is small and a little A-ward of the apex.

*Remarks.*—Ulrich & Bassler's type is a gerontic specimen, the blade of which (in the upper right lobe of fig. 18) is partly broken off. The species is distinguished from *A. princeps* by the median position of the blade and the less developed B-portion of carina. *A. calvini* has a wider keel angle, rounded lobes and stronger developed carina.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 10,11. Independence shale at the county farm near Independence, outcrop in the creek bed. Sweetland Creek shale near Muscatine, undifferentiated.

Hardin sandstone, Tennessee, Adorfer Kalk, Germany, Manticoceras beds, Australia.

*Figured specimens.*—SUI 8080, SUI 9967, SUI 9969, SUI 9970.

### ANCYROIDES CALVINI Miller & Youngquist

Pl. 138, fig. 6

v. *Ancyroides calvini* MILLER & YOUNGQUIST, 1947, Jour. Paleont., vol. 21, p. 504, pl. 75, fig. 4.

v. non! *Ancyroides calvini* YOUNGQUIST & MILLER, 1948, ibid., vol. 22, p. 441, pl. 68, fig. 16. [=*A. asymmetrica*?].

*Diagnosis.*—A representative of *Ancyroides* with the blade in the middle of A-lobe, a widely rounded, subsymmetrical plate, and distinct carina and secondary carina. The angle between B-portion of keel and secondary keel is obtuse.

*Description.*—Blade denticulate, short, near the middle of the A-lobe, stout, increasing strongly in height toward B, it ends abruptly in A-lobe. The first denticle is very small, so that a rim of the plate A-ward of blade is suggested. The plate is wide and little arched. Carina distinct and straight, A- and B-ward portions forming an obtuse angle. Sculpture of plate consists of quite coarse, regular, rounded nodes. The three lobes of plate have convex flanges. Lower side: escutcheon small, somewhat A-ward of the apex. Keel and secondary keel meet the rim in the center of the lobes. The keel angle is about 90–100°. The crimp is narrow.

*Occurrence.*—Amana beds at State Highway 220, near Middle Amana, layer 11. Sweetland Creek shale near Muscatine, upper layer at Campbell's Run, and undifferentiated in other outcrops.

*Figured specimen.*—SUI 9945.

### ANCYROIDES EUGLYPHEUS (Stauffer)
Pl. 138, fig. 7a,b

*Ancyrognathus euglypheus* STAUFFER, 1938, Jour. Paleont., vol. 12, p. 418, pl. 53, fig. 18.
v. *Ancyroides euglypheus* MILLER & YOUNGQUIST, 1947, ibid., vol. 21, p. 505, pl. 75, fig. 6.

*Diagnosis.*—A primitive *Ancyroides* with small plate, high, marginal blade, little developed C-lobe, distinct but shallow carina and secondary carina, and broad crimp.

*Description.*—The blade is strongly developed, very high and marginal on D-rim. The plate is small, little arched, and has a distinct, low regularly bowed carina (convex toward C), and a short secondary carina on the C-side. The lobe on C-side is only little developed; outline is thus similar to species of *Polygnathus.* The upper side of plate is adorned with regularly rounded nodes. The lower side has an obtuse keel angle, a small, elongate escutcheon at the apex and a broad crimp.

*Remarks.*—The outline of plate suggests that this species is close to *Polygnathus,* from which the genus may have originated.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 8. Sweetland Creek shale near Muscatine. Olentangy shale, Ohio.

*Figured specimen.*—SUI 9946.

### ANCYROIDES PRINCEPS Miller & Youngquist
Pl. 137, fig. 7

v. *Ancyroides princeps* MILLER & YOUNGQUIST, 1947, Jour. Paleont., vol. 21, p. 505, pl. 75, fig. 2,3. 3[=holotype].
v. *Ancyroides princeps* YOUNGQUIST & MILLER, 1948, ibid., vol. 22, p. 441, pl. 68, fig. 20.
v. ?*Ancyroides ornatissimus* YOUNGQUIST & MILLER, 1948, ibid., vol. 22, p. 441, pl. 68, fig. 18.

*Diagnosis.*—A representative of *Ancyroides* with the blade at the D-rim. The carinae are not well developed near the growth center, but increase in height toward the rim. Keel angle is less than 90°.

*Description.*—A fragmentary specimen has a well developed blade near the D-rim, and a secondary carina increasing toward the rim. The fairly broad crimp and small escutcheon on the lower side are in good agreement with the holotype. The keel angle is less than 90° on the holotype.

*Remarks.*—*A. ornatissimus* is based on a single specimen which resembles *A. princeps* in the keel angle and the marginal position of blade. Increase of the carinae toward the rim is somewhat stronger than is usual on *A. princeps,* of which it is probably only a gerontic, atypical specimen.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 8, with ?10,12. Sweetland Creek shale near Muscatine, upper layer at Campbell's Run.

*Figured specimen.*—SUI 9938.

### ANCYROIDES UDDENI Miller & Youngquist
Pl. 138, fig. 10a,b,11

*Ancyrognathus symmetrica* MEHL & QUIGLEY in Branson, 1944, Mo. Univ. Stud., vol. 19, no. 3, p. 153, pl. 26, fig. 28. (cet ex.)
v. *Ancyroides uddeni* MILLER & YOUNGQUIST, 1947, Jour. Paleont., vol. 21, p. 505, pl. 75, fig. 5. [non! pl. 74, fig. 16=*asymmetrica*].
v. *Ancyroides uddeni* YOUNGQUIST & MILLER, 1948, ibid., vol. 22, p. 442, pl. 68, fig. 15.

*Diagnosis.*—A representative of *Ancyroides* with median or submarginal blade, without or with faint carina and secondary

carina. Lobes blunt, keel angle acute, crimp broad.

*Description.*—Blade denticulate, relatively long, median, beginning right on the tip of the A-lobe. B-ward of the longest denticle are about 4 smaller ones which decrease in height toward the growth center of the unit. Plate is strongly arched with irregular outline, rims convex or straight. Sinus in the rim between B-end and C-lobe deep, its flanges are convex. Carina and secondary carina are faint or in some cases even absent. Sculpture of plate consists of regular, rounded nodes. The keel angle is on the largest figured specimen about 80°, on smaller ones even more acute. A small, elongate escutcheon is developed a little A-ward of the apex.

*Remarks.*—The species is close to *A. asymmetrica.* Differences are lack of carinae, more convex rims and the more blunt lobes. *A. calvini* has an obtuse keel angle and well developed carinae. *A. euglypheus* and *A. princeps* have a marginal blade.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 11; westernmost outcrop beneath the Pennsylvanian sandstone. Independence shale at the county farm near Independence, outcrop in the creek bed. Sweetland Creek shale near Muscatine. Sylamore sandstone, Missouri.

*Figured specimens.*—SUI 9947, SUI 9948.

### Genus PALMATOLEPIS Ulrich & Bassler, 1926

For synonymy, remarks on the type species, and the subgenera, see Müller, 1956a, p. 14.

*Diagnosis.*—Paired asymmetrical conodonts which are present as dextral and sinistral specimens in statistically equal numbers. They are compounds of a blade and a ±large platform. Blade on the A-side, ending with a slant which may or may not bear denticles. The greatest height of the blade is either on or behind the A-ward tip.

The blade is adorned with closely approximated denticles which (in most cases) have been only little enlarged but considerably increased in number during ontogeny. Rarely, the denticles may grow strongly, thus forming germ denticles. On gerontic specimens the denticles may form an irregular line on the upper side. In some species no denticles are developed at all. On the platform the blade tapers toward a carina which is ±straight, bowed (convex toward C) or sigmoidal, and decreases in height B-ward.

Like the blade, the carina is adorned with denticles. One is distinguished by its size, and in many cases by its odd position. This cone-shaped denticle (azygous node) is in the center of the growth lines. B-ward of the azygous node the carina in most cases forms an obtuse angle and tapers toward the B-tip, which is not always met.

A secondary carina may be developed; its highest point is either at the growth center or at the rim. The plate is "palmate," tongue shaped, or rounded-triangular; its largest portion is on the C-side of the unit. Single exception: *Pa.* (*Pa.*) *gonioclymeniae* which is ±undulate. The upper surface in most cases is adorned with a sculpture which on primitive species is arranged in radial rows centered in the azygous node. The A-D-portion of rim may be strengthened by a crest.

The lower side of plate has a crimp which was covered during the growth by the same tissue as the upper side. In a few species (*e.g.*, *Pa.* (*Deflectolepis*) *deflectens*) there is no crimp and the supporting tissue has covered a small margin of the upper side. The crimp is not as strongly sculptured as the upper side of plate and has a more or less shiny surface, in contrast to the basal portion which is without luster. On the basal portion in many specimens growth striae are visible which are formed by the edges of growth lamellae.

The center of the plate is in most cases the highest point of the lower side. In the middle of the unit beneath blade and carina there is developed a keel which is highest at the ends and in some cases is disconnected in the center. The azygous node on some specimens is visible on the lower side also. A secondary keel, corresponding to the secondary carina, if one is present, may be developed. It is restricted to the basal part and absent on the crimp. An escutcheon is rarely developed.

*Remarks.*—This genus is the predominant component in most of the assemblages studied here. All represented species belong to the subgenus *Manticolepis.*

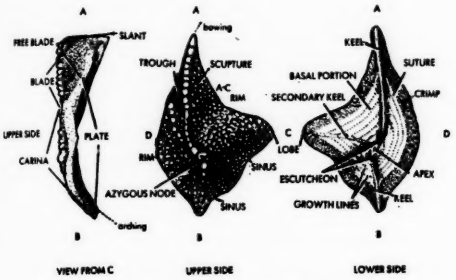
*Range.*—The genus seems to be restricted

to the Upper Devonian. Species are excellent time markers.

Subgenus MANTICOLEPIS Müller, 1956

*Subgenotype.*—*Palmatolepis subrecta* Miller & Youngquist, 1947.

*Diagnosis.*—Plate large and wide, the tip on the B-portion is arched downward, and forms the deepest point of the platform. There is a ±well developed C-ward lobe, its position may be either A-ward or B-ward of the azygous node. A secondary carina and a secondary keel may be present.




TEXT-FIG. 7—Morphology of *Palmatolepis* (*Manticolepis*).

PALMATOLEPIS (MANTICOLEPIS) AMANA Müller & Müller, n. sp.
Pl. 140, fig. 5

*Holotype.*—Original of Pl. 140, fig. 5.

*Locus typicus and stratum typicum.*—Amana beds at State Highway 220 near Middle Amana, layer 7.

*Derivatio nominis.*—After the type locality.

*Diagnosis.*—A representative of *Palmatolepis* (*Manticolepis*) with a high carina and distinct secondary carina, C-lobe is B-ward of the azygous node. Plate straight, with exception of the B-tip which is little arched downward.

*Description.*—Free blade large, slant on A-side nearly rectangular and undenticulate. Denticles irregular, broad and large. Carina high, ending abruptly in about the middle of distance between the azygous node and B-end. Secondary carina distinct, meets the rim near the center of C-lobe. Sculpture of plate consisting of irregular and unarranged nodes which increase in size toward the rim. Plate large and trilobate, straight, with the B-tip slightly arched downward. The D-rim is slightly convex, thus only a small portion of plate is D-ward of the carina. B-end short and blunt. The rim between B and C has one large sinus; C-lobe elongate, tongue shaped, tip is B-ward of the azygous node. The rim in A-C is concave.

Keel slightly sigmoidal, high on the ends and low in the center; a secondary keel is present. The crimp is fairly broad.

*Remarks.*—The color of the specimens is considerably darker than the usual preservation at the Amana locality. Primary occurrence in this formation therefore is not unquestioned, and the species may be a reworked component.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 7.

*Holotype.*—SUI 9959.

PALMATOLEPIS (MANTICOLEPIS) FLABELLIFORMIS (Stauffer)
Pl. 139, fig. 3–6; Pl. 142, fig. 9?

*Palmatolepis flabelliformis* STAUFFER, 1938, Jour. Paleont., vol. 12, p. 436, pl. 53, fig. 9, [=lectotype designated here], 12 [*cet. ex.*].
v. *Palmatolepis gigas* MILLER & YOUNGQUIST, 1947, ibid., vol. 21, p. 512, pl. 75, fig. 1.
*Palmatolepis subrecta* HASS, 1956, U. S. Geol. Surv. Prof. Paper, vol. 286, p. 17,19,20, pl. 3, fig. 12,14.
*Palmatolepis* sp. A. HASS, 1956, ibid., fig. 13.

*Diagnosis.*—A representative of *Palmatolepis* (*Manticolepis*) with large radially sculptured plate, distinct secondary carina and elongate C-ward lobe. Plate is arched, crimp broad.

*Description.*—Free blade fairly large. Blade straight, highest in the A-ward portion, slant steep and denticulate in the uppermost part only. Denticles large and irregular, ±fused on older growth stages. Carina slightly bowed toward C, A-ward of the azygous node which is large and distinct. B-ward of the azygous node it recurves toward D. Carina does not meet the tip; it tapers out behind the middle of the distance between azygous node and B-tip. Secondary carina distinct, highest near the azygous node and slightly bowed, convex toward A. The secondary carina ends on or behind the middle of the distance between azygous node and rim.

Plate large, strongly arched, the B-end

forming its deepest point. Sculpture consisting of numerous, elongate, radially arranged nodes which increase in prominence toward the rim.

The lower side has a broad crimp, a slightly sigmoidal keel, in some cases with a very small elongate escutcheon (Pl. 139, fig. 5b), and a secondary keel.

*Remarks.*—On the gerontic specimen figured on Pl. 139, fig. 6, the denticles of blade are grown together and form a jagged upper limit. The sculpture of plate consists of radially arranged ridges. The holotype of *Palmatolepis (Manticolepis) gigas* (Miller & Youngquist, 1947) is the only specimen found to date. It is regarded as belonging to *A. flabelliformis*, a large, atypical specimen.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 1–3, with ?5,6–8,10–13; westernmost outcrop beneath the Pennsylvanian sandstone. Independence shale at the county farm near Independence, outcrops at the crossroad and in the creek bed. Sweetland Creek shale near Muscatine, middle and upper layer at Campbell's Run. Filling of a sinkhole in Cedar Valley limestone at Solon. North Liberty beds 1½ miles northeast of North Liberty. Olentangy shale, Ohio.

*Figured specimens.*—SUI 9951–9954, SUI 9982.

### PALMATOLEPIS (MANTICOLEPIS) FOLIACEA (Youngquist)
Pl. 140, fig. 6–9

v. *Palmatolepis foliaceus* YOUNGQUIST, 1945, Jour. Paleont., vol. 19, p. 364, pl. 56, fig. 11,12. [12 = lectotype designated here].

*Diagnosis.*—A representative of *Palmatolepis (Manticolepis)* with a ±oval plate. The C-ward lobe is wide, flat and hardly differentiated by sinus on its flages. The keel is slightly sigmoidal, the crimp broad.

*Description.*—Free blade short. Blade not very high, slant fairly steep. Denticles large and irregular on larger specimens, small and regular on earlier growth stages. Carina relatively straight, somewhat sigmoidal. Azygous node well differentiated. No secondary carina is developed.

Plate fairly large, strongly arched, the B-tip forming the deepest point. D-rim regularly convex up to the pointed B-ward tip. Rim betweeen B and C convex on some specimens with a small sinus near the B-ward tip. C-lobe wide and only little differentiated, the rim between A and C ±straight with shallow indentations. Sculpture of plate consists of irregular nodes which in older growth stages occur as radial ridges. The keel is somewhat sigmoidal, the crimp broad; no escutcheon is present.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 1–8. Independence shale at the county farm near Independence, outcrop at the crossroad. North Liberty beds 1½ miles northeast of North Liberty.

*Figured specimens.*—SUI 9960–9963.

### PALMATOLEPIS (MANTICOLEPIS) HASSI
Müller & Müller, n. sp.
Pl. 139, fig. 2; Pl. 140, fig. 2,4

v. *Palmatolepis flabelliformis* YOUNGQUIST, 1945, Jour. Paleont., vol. 19, p. 364, pl. 56, fig. 1.
v. *Palmatolepis subperlobata* MILLER & YOUNG-

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### EXPLANATION OF PLATE 141

All specimens are from the Independence shale at the county farm near Independence, Buchanan Co., Iowa. Fig. 1 is from the outcrop at the crossroad; figs. 2–10 are from the outcrop in the creek bed. All figures are unretouched photographs, ×40.

FIG. *1*—*Polygnathus granulosa* Branson & Mehl. Dextral specimen; *a*, lateral view (from D), the lower portion of blade is not preserved; *b*, upper view. (See also Pl. 135, fig. 2,8.)

*2,9*—*Polygnathus independensis*, n. sp. *2*, holotype, dextral; *a*, upper view; *b*, lateral view (from D) with portions of the base, the A-ward part of blade is not preserved. *9*, dextral, atypical specimen.

*3*—*Polygnathus normalis* Miller & Youngquist. Sinistral specimen. (See also Pl. 135, fig. 9.)

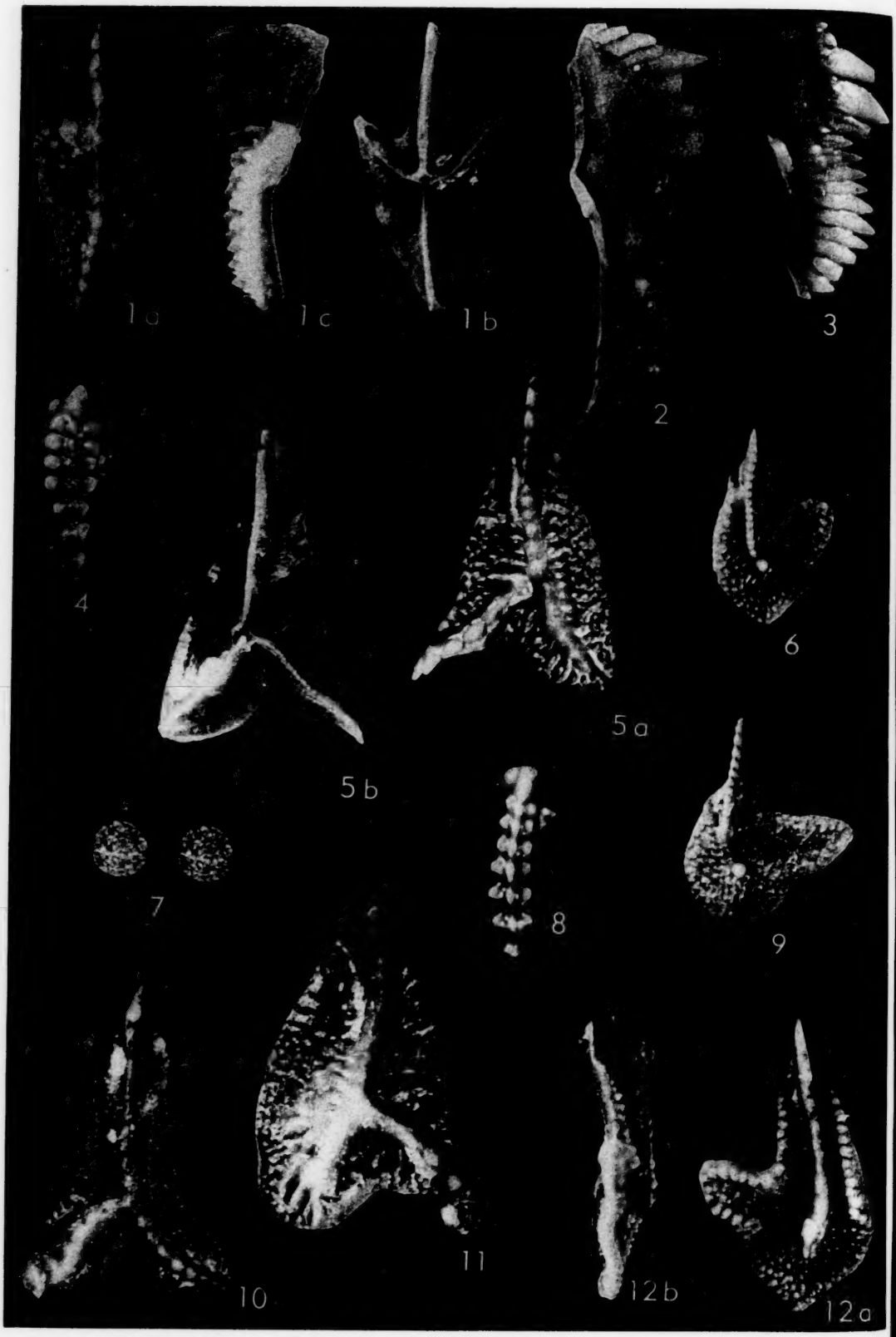
*4,6,7*—*Ancyroides asymmetrica* (Ulrich & Bassler). *4*, sinistral specimen. *6*, dextral specimen. *7*, holotype dextral. (See also Pl. 4, fig. 8,9.)

*5*—*Ancyrognathus* aff. *A. alta*, n. sp. Dextral specimen; *a*, upper view; *b*, lower view; *c*, lateral view (from C). (Comp. with Pl. 4, fig. 4.)

*8*—*Ancyrodella gigas* Youngquist. Sinistral specimen; the blade is not preserved. (See also Pl. 142, fig. 1.)

*10*—*Polygnathus unicornis*, n. sp. Sinistral specimen; the secondary keel is regarded as due to abnormal growth. (See also Pl. 135, fig. 5,7.)

1a
1b
2a
2b
3
4
5a
5c
5b
6
7
8
9
10


1a
1c
1b
3
2
4
5
6
5a
5b
7
8
9
10
11
12b
12a

QUIST, 1947, ibid., vol. 21, p. 513, pl. 75, fig. 13,14, [non! 12].

*Palmatolepis subrecta* HASS, 1951, Bull. Amer. Assoc. Petrol. Geol., vol. 35, p. 2531, pl. 1, fig. 19.

*Holotype.*—Original of Pl. 140, fig. 4.

*Locus typicus and stratum typicum.*—Amana beds at State Highway 220 near Middle Amana, layer 7.

*Derivatio nominis.*—In honor of Dr. Wilbert H. Hass, Washington, D. C.

*Diagnosis.*—A representative of *Palmatolepis* (*Manticolepis*) with a large strongly arched trilobate plate. The position of C-ward lobe is A-ward of the azygous node. The blade is relatively flat, the carina and keel sigmoidal. A secondary keel is often present although a secondary carina is not. An escutcheon is commonly developed.

*Description.*—Free blade short, one-fourth to one-fifth of the length between A-ward tip and azygous node. Blade of medium height, slant fairly steep and little denticulate. Carina sigmoidal. Azygous node well differentiated from the small, regular and discrete denticles. Carina tapers out shortly B-ward of the azygous node, but in some cases a faint dotted line goes to the tip. Plate large and trilobate, strongly arched. D-rim regularly convex up to the B-tip, where a small sinus may be developed. It may have a ridge on the A-ward portion. B-end pointed to blunt, forming the deepest point of the plate. In the rim between B and C characteristically two sinuses near the tips are developed. C-lobe large, rounded and A-ward of the azygous node in position, rim in A–C regularly concave. Sculpture of plate consists of irregular nodes which in some cases are faintly arranged in radial rows

Lower side: keel sigmoidal, in some cases with a small oval escutcheon in the growth center, keel highest at the tips, but always connected in the center. Secondary keel faint, in some cases absent. The crimp is broad.

*Remarks.*—This species is close to *Palmatolepis subrecta* Miller & Youngquist, from which it may be distinguished by the ordinarily absent secondary carina, the less sigmoidal keel, the common presence of an escutcheon and particularly by the more A-ward position of the C-lobe. *Palmatolepis subperlobata* is distinct by the upward arching of the B-ward tip of plate.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 1–9, with ?10,12; westernmost outcrop beneath the Pennsylvanian sandstone. Independence shale at the county farm near Independence, outcrop at the crossroad. Limestone bed in Independence shale at Brandon. Sweetland Creek shale near Muscatine, middle layer at Campbell's Run, and undifferentiated in other outcrops. Filling of a sinkhole in Cedar Valley limestone at Solon. North Liberty beds 1½ miles northeast of North Liberty.

*Types.*—Holotype SUI 9958; figured paratypes SUI 9950, SUI 9956, SUI 9957.

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EXPLANATION OF PLATE 142

All specimens are from the North Liberty beds 1½ miles northeast of North Liberty, Johnson Co., Iowa. All figures are unretouched photographs, ×40.

FIG. *1—Ancyrodella gigas* Youngquist. Sinistral specimen; *a*, upper view; *b*, lower view; *c*, lateral view (from C). (See also Pl. 141, fig. 8.)
*2,3—Ctenognathus* (*Pandorinellina*) *insita* (Stauffer).
*4—Icriodus expansus* Branson & Mehl. Dextral specimen.
*5—Ancyrognathus bifurcata* (Ulrich & Bassler). Dextral specimen; *a*, upper view; *b*, lower view. (Comp. with Pl. 142, fig. 11).
*6—Palmatolepis* (*Manticolepis*) *martenbergensis* Muller. Sinistral specimen.
*7—Tasmanites* sp. Two compressed specimens.
*8—Icriodus symmetricus* Branson & Mehl. Dextral specimen. (See also Pl. 138, fig. 1–3.)
*9—Palmatolepis* (*Manticolepis*) *flabelliformis* (Stauffer)? Sinstral, small specimen. (Comp. with Pl. 139, fig. 3–6.)
*10—Ancyrognathus* sp. *A*. Dextral specimen.
*11—Ancyrognathus bifurcata* (Ulrich & Bassler)? Sinistral specimen. (Comp. with Pl. 142, fig. 5.)
*12—Palmatolepis* (*Manticolepis*) sp. Dextral specimen; *a*, upper view; *b*, lateral view (from C).

PALMATOLEPIS (MANTICOLEPIS) MARTENBERGENSIS Müller
Pl. 142, fig. 6

*Palmatolepis (M.) martenbergensis* MÜLLER, 1956, Abh. Senckenberg. Naturf. Ges., vol. 494, p. 19, pl. 1, fig. 3–8; pl. 2, fig. 10–13.

In Europe this species is restricted to the lower and middle portion of *Manticoceras*-Stufe. Its occurrence in the North Liberty shale is an indication that in these beds an equivalent of the middle Frasnian is included.

*Occurrence.*—North Liberty beds 1½ miles northeast of North Liberty. Lower and middle part of Adorf-Stufe, Germany.

*Figured specimen.*—SUI 9980.

PALMATOLEPIS (MANTICOLEPIS) SUBRECTA Miller & Youngquist)
Pl. 139, fig. 1

?*Palmatolepis flabelliformis* STAUFFER, 1938, Jour. Paleont., vol. 12, p. 436, pl. 53, fig. 4.
v. *Palmatolepis subrecta* MILLER & YOUNGQUIST, 1947, ibid., vol. 21, p. 513, pl. 75, fig. 7–11. [8=lectotype designated here].
v. *Palmatolepis subrecta* YOUNGQUIST & MILLER, 1948, ibid., vol. 22, p. 448, pl. 68, fig. 17.

*Diagnosis.*—A representative of *Palmatolepis* (*Manticolepis*) with little arched elongate-triangular plate. The position of C-ward lobe is of about the same height as the azygous node. Carina and keel are strongly sigmoidal. A secondary carina is slightly developed; a secondary keel is present.

*Description.*—Free blade short. Blade straight and shallow, denticles regularly rounded and short. Carina strongly sigmoidal, curves only shortly A-ward of azygous node. Plate elongate, trilobate and only little arched, the B-ward tip forming its deepest point. D-rim convex; it may have a ridge on the A-portion. B-end pointed. Rim between B and C with 1–2 sinus. C-lobe in about the same height as the azygous node, fairly narrow and rounded. Rim between A and C concave. Sculpture consists of fine nodes which are equally distributed over the plate. The lower side has a strongly sigmoidal keel, and secondary keel. The crimp is broad.

*Remarks.*—For comparison see description of *Palmatolepis hassi* and Müller (1956a, p. 22).

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, ?layer 9, layer 10–13. Independence shale at the county farm near Independence, outcrop in the creek bed. Sweetland Creek shale near Muscatine, upper layer at Campbell's Run. Olentangy shale, Ohio?

*Figured specimen.*—SUI 9949.

PALMATOLEPIS (MANTICOLEPIS) UNICORNIS (Miller & Youngquist)
Pl. 140, fig. 1

v. *Palmatolepis unicornis* MILLER & YOUNGQUIST, 1947, Jour. Paleont., vol. 21, p. 514, pl. 75, fig. 15 (holotype).

*Diagnosis.*—A representative of *Palmatolepis* (*Manticolepis*) with an exceptionally high blade, rounded C-ward lobe and a secondary carina.

*Description.*—Free blade large. Blade extremely high, with large denticles, slant steep and undenticulate. Carina distinct with large denticles. Secondary carina always present, partly broken off on the figured specimen. Plate large and trilobate, somewhat arched. D-rim convex, in some cases with numerous indentations, B-tip pointed and forming the deepest portion of the plate. Rim in B-C with two shallow sinus, C-lobe widely rounded but distinctly separated. Rim in A-C strongly concave. Sculpture consists of rounded and large nodes which are most strongly developed near the rim. Lower side: crimp narrow, secondary keel distinct.

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 1,6,10. Independence shale at the county farm near Independence, outcrop in the creek bed. Sweetland Creek shale near Muscatine, middle layer at Campbell's Run, and undifferentiated in other outcrops.

*Figured specimen.*—SUI 9955.

PALMATOLEPIS (MANTICOLEPIS) sp.
Pl. 142, fig. 12

*Palmatolepis marginata* YOUNGQUIST, 1947, Jour. Paleont., vol. 21, p. 108, pl. 24, fig. 4,14.
*Palmatolepis* sp., ibid., p. 108, pl. 24, fig. 5.

Plate fairly large, D-rim is strongly convex and has a distinct ridge on the A-ward portion which extends about until the azygous node. B-end blunt. The B-C-rim is straight or has a small sinus near the C-lobe which is pointing strongly toward

A. A-C-rim is strongly concave-angulate.

Sculpture of plate consists of irregularly arranged nodes which increase in size toward the rim. Troughs are well developed and steep. The keel is slightly sigmoidal; no secondary keel is present. The crimp is fairly narrow.

*Occurrence.*—Independence shale in Benton County Sec. 9, T86N, R6W. Sweetland Creek shale near Muscatine, lower layer at Campbell's Run. North Liberty beds 1½ miles northeast of North Liberty.

*Figured specimen.*—SUI 9985.

## Family Icriodidae Müller & Müller, n. fam.

*Diagnosis.*—Platform and blade types with a large and deep basal cavity which extends over the entire length of unit and forms a loop beneath the blade or its homologue, the main cusp. The upper surface is adorned with 1–3 rows of denticles which may be connected by ridges, but has no other sculpture.

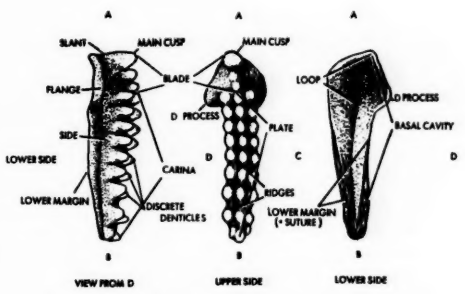
*Remarks.*—Branson & Mehl, 1944, p. 245, have referred *Icriodus* to the Gnathodontidae. They stated that *Icriodus* does not have a blade. However, this is true only in the more advanced forms on which it has been reduced to a main cusp.

Primitive forms like *Icriodus brevis* Stauffer, 1940, *Icriodus angustus* Stewart & Sweet, 1956, *Icriodus cymbiformis* Branson & Mehl, 1938, and *Icriodus latericrescens* Branson & Mehl, 1938, demonstrate that in this genus the basal cavity is well developed beneath the blade and tapers toward the end opposite to the blade (which is designated B). In the Gnathodontidae the basal cavity is restricted to the B-ward portion beneath the platform, and the blade is free. This fundamental difference makes it necessary to establish a suprageneric taxon.

*Pelekysgnathus* Thomas, 1949, resembles *Icriodus* in basal cavity, main cusp, as well as the height of the sides, but has developed only one row of denticles on the upper surface.

*Polygnathus hulkus* Stauffer, 1940, has a basal cavity beneath the blade and therefore may belong to an undescribed genus of Icriodidae.

*Recorded range.*—Lower-Upper Devonian.




TEXT-FIG. *8*—Morphology of *Icriodus*.

## Genus Icriodus Branson & Mehl, 1938

*Type species.*—*Icriodus expansus* Branson & Mehl, 1938.

*Diagnosis.*—(Modified after Branson & Mehl, 1938, p. 159; changes are italicized.) Platformlike *units* with high sides either straight or flaring near the lower margin, of more or less spindle-shaped or lachrymiform outline in *upper* view, modified in some forms by *one or more* laterally projecting processes at the *A-end* and *often* without a distinct *blade, but with a more or less prominent main cusp.* The *upper* side consists of two (*rare*) *or three* (*in most cases*) longitudinal rows of low *denticles.* The *lower* side is deeply excavated its entire length. *The greatest width is in a loop beneath the main cusp or blade.*

*Remarks.*—The genus was described in 1934 with *Icriodus expansus* as type—a nomen nudum until 1938. Therefore, according to art. 25 of the International Rules of Zoological Nomenclature the valid date for establishing the genus is 1938.

The following features in various combinations are useful for definition of species: number and form, or absence of lateral branches; presence or absence of blade; arrangement, form and size of the denticles; differences between the median and lateral rows (*e.g.*, corresponding or alternate); presence of ridges between the denticles in either longitudinal or vertical direction (or both); degree of symmetry and regularity of the denticles; size and shape of loop; height of sides; development of a lateral furrow; position of greatest width of the plate (*e.g.*, on A-side or in the middle of unit); degree of flaring of the sides toward the lower limit.

Species of this partial-genus may be useful for definition of zones.

*Occurrence.*—Lower-Upper Devonian in North America, Europe, and Australia. Common, locally abundant.

### Icriodus expansus
Branson & Mehl
Pl. 142, fig. 4

*Icriodus expansus* Branson & Mehl, 1938, Jour. Paleont., vol. 12, p. 160, pl. 26, fig. 18–21.
v. *Icriodus subterminus* Youngquist, 1947, ibid., vol. 21, p. 103, pl. 25, fig. 14.
*Icriodus expansus* Fay, 1952, Kansas Univ. Pal. Contrb., art. 3, p. 110, [gives extensive occurrences].
*Icriodus* sp. Hass, 1956, U. S. Geol. Surv. Prof. Paper, vol. 286, tab. 7,8, pl. 4, fig. 6.

The recorded range of this species is Middle Devonian-Middle Frasnian. Its occurrence in North Liberty shale is an indication that these beds are partly equivalent to the Middle Frasnian in Europe.

*Occurrence.*—North Liberty beds 1½ miles northeast of North Liberty.

*Figured specimen.*—SIU 9978.

### Icriodus symmetricus
Branson & Mehl

*Icriodus symmetricus* Branson & Mehl, 1934, Univ. Missouri Studies, vol. 8, p. 226, pl. 13, fig. 1–3.
*Icriodus symmetricus* Branson & Mehl, 1938, Jour. Paleont., vol. 12, p. 161, pl. 26, fig. 1–3.
*Icriodus symmetricus* Branson & Mehl, 1944, *in* Shimer & Shrock, Index fossils of North America, p. 245–246, pl. 94, fig. 65.
*Icriodus symmetricus* Branson, 1944, Univ. Missouri Studies, vol. 19, no. 3, p. 157,163, pl. 28, fig. 1–3, p. 173 [admixture?].
v. *Icriodus symmetricus* Youngquist, 1947, Jour. Paleont., vol. 21, p. 103, pl. 25, fig. 5.
*Icriodus symmetricus* Beckmann, 1949, Senckenbergiana, vol. 30, p. 155, pl. 1, fig. 6; pl. 3, fig. 1; pl. 4, fig. 5.
*Icriodus* sp. Hass, 1951, Amer. Assoc. Petrol. Geol., Bull., vol. 35, p. 2531,2534–35, pl. 1, fig. 17.

*Diagnosis.*—A representative of *Icriodus* with three rows of regular, rounded denticles which also form lateral rows. The median row is the highest; its denticles are connected by a shallow longitudinal ridge. The sides are subparallel.

*Description.*—A-ward cusp not much larger than other denticles. Blade fairly distinct, consisting of three denticles. Plate with three rows of regularly shaped denticles, the median one is the highest. Platform slender, elongate, slowly tapering toward B, its sides are subparallel, the axis is slightly bowed. The lower surface has a basal cavity with a fairly wide flared loop on A-side, and tapers toward the B-tip.

*Recorded range.*—This species seems to be confined to the higher portion of early Upper Devonian (correlative of the *Manticoceras* beds) but lacks in its lowermost zone (correlative of *Koenenites* beds).

*Occurrence.*—Amana beds at State Highway 220 near Middle Amana, layer 2,3,7,8. Independence shale at the county farm near Independence, outcrops at the crossroad and in the creek bed. Sweetland Creek shale near Muscatine, lower, middle and upper layer at Campbell's Run. North Liberty beds 1½ miles northeast of North Liberty.

Woodford shale Oklahoma?; Sylamore sandstone, Arkansas; Arkansas novaculite, Arkansas; Grassy Creek shale, Missouri, Illinois; Huron, Ohio?; Iberger Kalk, Germany.

*Figured specimens.*—SUI 9939–9941, SUI 9981.

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# CORRELATION OF THE GULF AND ATLANTIC COASTAL PLAIN PALEOCENE AND LOWER EOCENE FORMATIONS BY MEANS OF PLANKTONIC FORAMINIFERA

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ABSTRACT—Stages and formations at the Cretaceous-Tertiary boundary are discussed on the basis of their type localities and their equivalents in other regions, with evidence presented as to the stratigraphic value of their planktonic foraminiferal assemblages for local and interregional correlation. The planktonic assemblages are recognized to be of worldwide extent; the stages each have a characteristic generic aspect.

The *Globotruncana* assemblage is characteristic of Upper Cretaceous strata, and is followed by a nearly complete change in generic character in later beds. An identical *Globigerina* assemblage occurs in the type Danian, in the type Montian, and in the lower part of the Midway group. The Danian is therefore regarded as of early Paleocene age; the Landenian (upper Paleocene) contains a *Globigerina*-keeled *Globorotalia* assemblage, and the Ypresian (lower Eocene) has a *Globigerina*-keeled *Globorotalia-Truncorotaloides* assemblage. A more detailed zonation at the specific level is proposed. The planktonic assemblages are here utilized for age determination and correlation of the Brightseat and Aquia formations of Maryland and Virginia, the Hornerstown and Vincentown formations of New Jersey, the Midway group of the Gulf Coast area, and the Salt Mountain and Nanafalia formations of Alabama. These strata are correlated with others in Mexico, the Caribbean area, western Europe, the Middle East, and North Africa. The stratigraphic nomenclature and age designations in this report do not necessarily follow the usage of the U. S. Geological Survey.

## INTRODUCTION AND ACKNOWLEDGMENTS

THERE is little agreement as to the exact geologic age of most strata throughout the world that are equivalent in age to those stages in the standard European time scale between the Upper Cretaceous Maestrichtian and the Eocene Ypresian. A considerable part of the difficulty arises because of the necessity of correlating sediments elsewhere, which may be of lithologic and faunal facies quite different from those at the type regions of these stages of the European time scale. These type localities are in some instances of an extremely specialized nature. Thus one may need to correlate an offshore marine section with a reefal limestone of another area, tropical faunas with boreal ones, or marine strata with nonmarine ones. This difficulty is further amplified when correlation within marine sequences is based wholly on benthonic organisms, whose existence is affected by the local depth, temperature and salinity of the water, the character of the ocean bottom, amount of light and food available, and quantity of suspended sediments. The rate of evolution and the rate of dispersal of the various types of organisms are also important factors in their eventual value as index fossils. We do not intend to imply that megafossils are not extremely valuable in correlations, but there are unfortunately many areas of relatively deep water deposits where megafossils are almost nonexistent.

Because of their independence of the sea bottom, rapid dispersal by ocean currents, and their ability to select the depth and therefore to some extent the temperature they prefer while living, their relatively rapid evolutionary development, and their buoyancy which allows further current dispersal even after death of the organism, certain planktonic forms supply the best available evidence for world-wide correlations.

Thus, the value of the probably pelagic ammonites for chronologic use in the Mesozoic has been widely recognized for many years. They became extinct at the close of the Cretaceous (Maestrichtian), however, and the problematic sequence of strata at

the Cretaceous-Tertiary boundary, of Danian age and younger, contains no ammonites to aid in age determinations.

In recent years, the European students in particular have demonstrated the equally valuable part played by another group of pelagic organisms, the planktonic Foraminifera. They have been generally ignored in this country as stratigraphic tools and only an occasional species has been recorded or described, with little comment as to their value. A recent revision of the planktonic genera and families of Foraminifera (Bolli, Loeblich & Tappan, 1957), showed their potential value for stratigraphic use in the Cretaceous and Cenozoic, even on the generic level, and numerous articles by European and Caribbean workers have demonstrated their value for detailed zonation at the specific level.

The present paper has resulted from a study of the planktonic Foraminifera of the Paleocene and lowermost Eocene strata of the Atlantic and Gulf Coastal plain (Loeblich & Tappan, 1957). As a basis for discussion of the correlation of these formations with those of other areas, one must consider the basis for separation of the various stages, formations, and faunal zones elsewhere. The first portion of this paper therefore consists of a brief outline of the stratigraphic application of the planktonic Foraminifera. An examination of the Cretaceous-Tertiary boundary problem follows, with a general discussion of the uppermost Cretaceous, Paleocene, and lower Eocene stages and formations in various regions. The final portion of the paper consists of a summary of the stratigraphic conclusions and paleontologic zonations resulting from this study. This paper was presented April 2, 1957, at the symposium on biostratigraphy, Society of Economic Paleontologists and Mineralogists, St. Louis, Missouri; publication is authorized by the Director, U. S. Geological Survey.

This paper is the result of a study of the planktonic Foraminifera and their stratigraphic application, at the U. S. National Museum, for which technical assistants and illustrators have been in part financed by grants-in-aid of research from California Research Corporation, Carter Oil Company, Gulf Oil Corporation, and Humble Oil and Refining Company, to whom we express our gratitude.

Many of the samples used in the present study were collected by the present writers with the aid and guidance of other geologists: Messrs. David Carter and Wallace Pitcher, Imperial College, London, accompanied us in collecting the Thanet sands at Herne and Pegwell Bays, Kent County, England. M. Henri Tintant, Université de Dijon, France, accompanied us in the Paris Basin, in collecting the "calcaire pisolithique" (Montian) in contact with the Cretaceous chalk at Vigny, Dept. Seine-et-Oise, France, and the Sables de Bracheaux (type Paleocene) at the Butte de la Justice, near Bracheaux, Dept. Seine-et-Oise, France. In southwestern France, M. Roger Duperier, Musée de la Mer, Biarritz, France, directed the present writers in collecting the Danian and Paleocene in the Biarritz seacliffs. Messrs. J. H. van Voorthuysen, van der Heide, and van der Vaals of the Netherlands Geological Survey and Mr. Jan Hofker of The Hague, Netherlands, accompanied the writers in collecting from the type Maestrichtian and other Cretaceous strata in southern Limburg and adjacent regions of Belgium.

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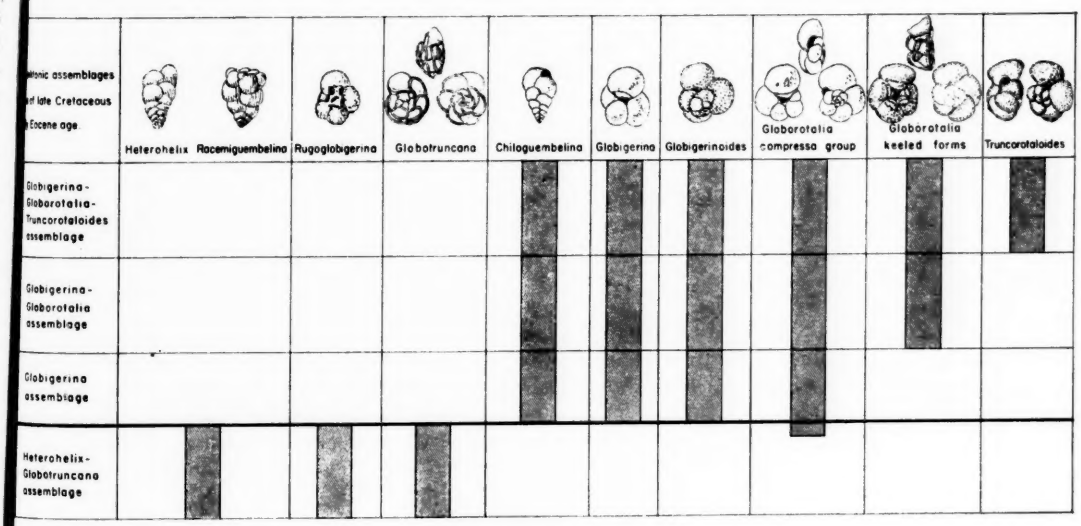
Samples and identified specimens from the Esna shale of Egypt in the U. S. National Museum have been collected by Drs. L. W. LeRoy, Colorado School of Mines, Golden, Colorado, and S. E. Nakkady, Alexandria University, Alexandria, Egypt.

## THE PLANKTONIC SUCCESSION AND ITS STRATIGRAPHIC VALUE

*Planktonic succession.*—Under a recent classification (Bolli, Loeblich & Tappan, 1957), four families are recognized for the coiled planktonic Foraminifera: the Hantkeninidae, Orbulinidae, Globorotaliidae and Globotruncanidae. There is one basically biserial planktonic family, the Heterohelicidae (revised by Gallitelli, 1957).

The Cretaceous planktonic assemblage is characterized by the following genera of the family Hantkeninidae, subfamily Planomalininae: *Globigerinelloides, Planomalina, Hastigerinoides, Biglobigerinella. Schackoina* represents the subfamily Hantkenininae. The Globorotaliidae is represented by *Praeglobotruncana* and *Rotalipora;* the Orbulinidae by *Globigerina,* and the Globotruncanidae by *Globotruncana, Rugoglobigerina* and *Abathomphalus.* The Heterohelicidae is almost completely a Cretaceous family, and contains the genera *Guembelitria, Guembelitriella, Heterohelix, Pseudotextularia, Pseudoguembelina, Gublerina, Planoglobulina, Racemiguembelina,* and *Tubitextularia.* Most of the above mentioned genera became extinct at the close of the Cretaceous. Thus the subfamily Planomalininae is represented only by local occurrences of *Biglobigerinella* in the Paleocene; the Globotruncanidae are completely extinct; and all but *Heterohelix* and *Tubitextularia* of the Cretaceous Heterohelicidae have disappeared. This Cretaceous assemblage is referred to as the *Heterohelix-Globotruncana* assemblage (Text-fig. 1).

In the Tertiary a new expansion of the planktonic Foraminifera occurs, representing in general different subfamilies than those of the Cretaceous. *Globigerina* and *Globigerinoides* (Orbulinidae), and *Globorotalia* (Globorotaliidae), are the only coiled planktonic genera in the Paleocene (Danian through Thanetian). The Heterohelicidae show a slight expansion, with the development of *Chiloguembelina* and *Woodringina,* in association with the few remaining *Heterohelix* and *Tubitextularia.* This restricted assemblage is termed the *Globigerina* assemblage. The Paleocene thus has the most re-




TEXT-FIG. 1

the Cretaceous-Tertiary boundary, of Danian age and younger, contains no ammonites to aid in age determinations.

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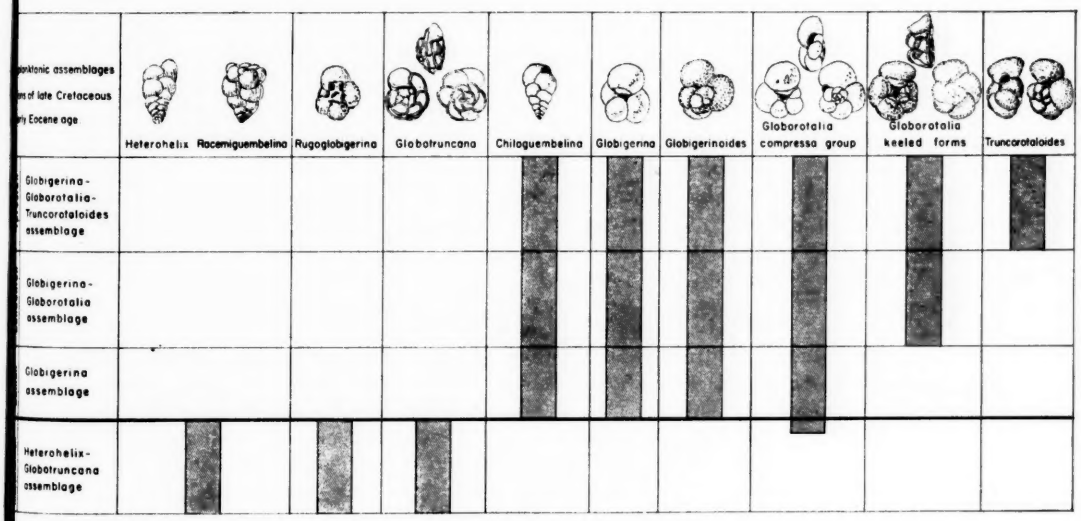
The Cretaceous planktonic assemblage is characterized by the following genera of the family Hantkeninidae, subfamily Planomalininae: *Globigerinelloides, Planomalina, Hastigerinoides, Biglobigerinella. Schackoina* represents the subfamily Hantkenininae. The Globorotaliidae is represented by *Praeglobotruncana* and *Rotalipora;* the Orbulinidae by *Globigerina,* and the Globotruncanidae by *Globotruncana, Rugoglobigerina* and *Abathomphalus.* The Heterohelicidae is almost completely a Cretaceous family, and contains the genera *Guembelitria, Guembelitriella, Heterohelix, Pseudotextularia, Pseudoguembelina, Gublerina, Planoglobulina, Racemiguembelina,* and *Tubitextularia.* Most of the above mentioned genera became extinct at the close of the Cretaceous. Thus the subfamily Planomalininae is represented only by local occurrences of *Biglobigerinella* in the Paleocene; the Globotruncanidae are completely extinct; and all but *Heterohelix* and *Tubitextularia* of the Cretaceous Heterohelicidae have disappeared. This Cretaceous assemblage is referred to as the *Heterohelix-Globotruncana* assemblage (Text-fig. 1).

In the Tertiary a new expansion of the planktonic Foraminifera occurs, representing in general different subfamilies than those of the Cretaceous. *Globigerina* and *Globigerinoides* (Orbulinidae), and *Globorotalia* (Globorotaliidae), are the only coiled planktonic genera in the Paleocene (Danian through Thanetian). The Heterohelicidae show a slight expansion, with the development of *Chiloguembelina* and *Woodringina,* in association with the few remaining *Heterohelix* and *Tubitextularia.* This restricted assemblage is termed the *Globigerina* assemblage. The Paleocene thus has the most re-




TEXT-FIG. 1

stricted generic assemblage of planktonic Foraminifera since the mid-Cretaceous. In the Danian, even *Globorotalia* is represented only by species which seem transitional from *Globigerina*, with rounded rather than keeled periphery, but with an extraumbilical aperture such as that of true *Globorotalia*.

More typical angular *Globorotalia* appear in the middle and late Paleocene, in association with the other genera continuing from the Danian. This assemblage is termed the *Globigerina-Globorotalia* assemblage. In the lower Eocene, *Truncorotaloides* appears, giving the name to this lower Eocene faunal assemblage. In the middle Eocene occurred an almost explosive expansion of the planktonic genera, with the development of *Hantkenina*, *Clavigerinella*, *Hastigerina*, *Globigerapsis*, *Porticulasphaera* and *Globigerinatheka*, and in the upper Eocene first appeared *Cribrohantkenina*, *Catapsydrax* and *Globoquadrina*. Many of these genera are restricted to the Eocene. *Cassigerinella* occurs only in the Oligocene and Miocene, and *Sphaeroidinella*, *Orbulina*, *Tinophodella*, *Globigerinita*, *Hastigerinella*, *Candeina*, *Globigerinoita* and *Globigerinatella* all appear in the Miocene, the last two being restricted to the Miocene. *Pulleniatina* first appeared in the Pliocene.

These and other genera are discussed by Bolli, Loeblich, and Tappan (1957), the above brief outline serving only to emphasize their value as age indicators.

*Stratigraphic value.*—Grimsdale (1951, p. 464,465), at the 3rd World Petroleum Congress, stated that the pelagic Foraminifera have most of the requisites of "ideal geological zone fossils—abundance, wide and rapid dispersal," etc., and that his stratigraphic work in the Middle East was based mainly upon the sequence of pelagic species, which he and others found to provide the most reliable means of age determination in the Tertiary rocks.

In contrast to this commonly accepted belief in the value of the planktonic Foraminifera, Todd (1954, p. 448) stated that "The planktonic species, however, are generally limited in their occurrence to open-sea facies and, thus, are available for correlation only between such facies." Later in the same article, in discussing the benthonic Foraminifera, she stated that dead shells are easily distributed by currents or by gravity some distance from their actual living sites. Certainly this is equally true of the planktonic species, which are current distributed both when living and dead. Abundant dead specimens of planktonic species occur in Recent Pacific lagoonal samples studied by the writers, and these species certainly were not living there. In strata examined for this study we have found the same species of planktonic Foraminifera in fine grained sediments such as the upper Lizard Springs formation of Trinidad, which contains a typical offshore and deepwater planktonic assemblage and in such shallow water deposits as the *Ostrea thirsae* beds of the Nanafalia formation of Alabama. They may occur in sandy strata, greensands, red clays or bryozoan limestones and their contemporaneity is attested to by the same sequence of assemblages and faunal zones in Africa, Europe, Asia and North America regardless of these local facies. They thus appear in contemporaneous sediments of varying facies, but as they live largely in the surface waters, they were not controlled by these bottom environments. They may not even have actually lived in each of the local areas, but may have been carried in after death.

Although, perhaps of less value as ecologic indicators, the planktonic forms are certainly better horizon indicators than many of the more provincial benthonic species. As was stated by Bolli (1957):

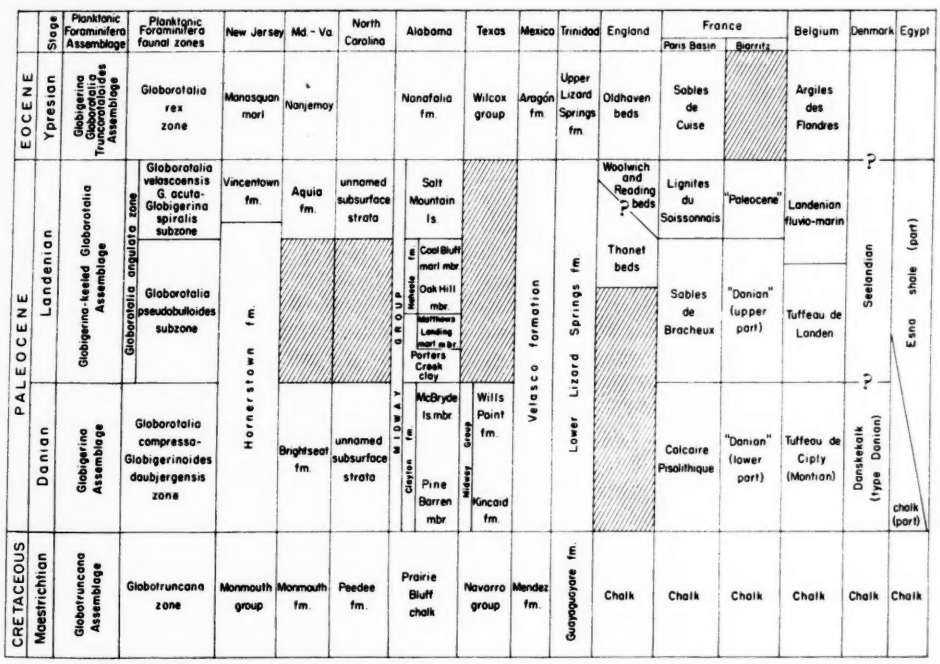
> The complete change of the planktonic foraminiferal fauna between the Upper Cretaceous . . . and the Paleocene . . . is not followed by the benthonic Foraminifera. . . . As many as about two-thirds of the benthonic species known in the Upper Cretaceous continue into the Paleocene-Lower Eocene. In cases where only benthonic Foraminifera are present, it may, therefore, become difficult to determine whether a fauna is of Upper Cretaceous or Paleocene age."

In all paleontologic work, care must be taken to recognize reworked specimens from older or underlying strata, or contamination of an outcrop by slumping from higher strata. Thus a few inconsistent records of planktonic species do occur in the literature which must be checked. The few Cenozoic records of *Globotruncana* are either examples of reworking, or due to contamination of outcrop or samples. *Globotruncana* has been

reported from the Eocene (Bettenstedt & Wicher, 1955), the Oligocene of Cuba (Palmer, 1940, p. 23), and even from Recent shore sands (*Globotruncana linneiana* d'Orbigny). Bettenstedt & Wicher (1955, p. 516) state that "*Globotruncana* sporadically continues to exist up to the lower Eocene." They doubted that it was due to reworking as all specimens found were relatively small, and there were no large specimens such as are typical of the Maestrichtian species. It would be interesting to learn if these specimens were referable to a Maestrichtian species, if they are true *Globotruncana*, for there is a possibility of a mechanical sorting of specimens of a single size in the process of reworking, just as the sediments are sorted by grain size. Overwhelming evidence throughout the world indicates a definite and almost simultaneous change in the planktonic generic assemblage at the Maestrichtian-Danian contact.

A few localities of very late Cretaceous (e.g., Redbank formation of New Jersey) do show specimens similar to *Globorotalia compressa* (Plummer) in association with an otherwise typical Cretaceous fauna, but it is to be expected that some transitional beds will be found occasionally. Furthermore, one or two localities of earliest Paleocene age (Hornerstown formation of New Jersey) show relict specimens of *Biglobigerinella* which is otherwise restricted to the Cretaceous. They represent a different species, and cannot be reworked specimens. These forerunners or relict specimens occur only near a contact and thus do not destroy the general value of the planktonic succession.

In a recent study of Atlantic and Gulf Coast Paleocene formations, a more detailed zonation was made on the basis of planktonic species (Text-fig. 2). The lowest zone, equivalent in age to the type Danian and type Montian, represents a "*Globigerina*" assemblage and is characterized by the species *Globorotalia compressa* and *Globigerinoides daubjergensis* (Bronnimann) which are restricted to this zone. Other species found in this zone include *Globorotalia pseudobulloides* (Plummer), *Chiloguembelina morsei*




TEXT-FIG. 2—Correlation of latest Cretaceous, Paleocene and lowermost Eocene strata of the Gulf and Atlantic Coastal Plains, and other selected regions, based on their planktonic foraminiferal assemblages.

(Kline), *Woodringina claytonensis* Loeblich & Tappan, *Globorotalia perclara* Loeblich & Tappan, and *Globigerina triloculinoides* Plummer, some of which also range somewhat higher in the Paleocene, but none of which persists until the lower Eocene. This zone is found in both the Kincaid and Wills Point formations of Texas, the Pine Barren and McBryde limestone members of the Clayton formation of Alabama (all of which are placed in the Midway group), in unnamed subsurface horizons drilled in North Carolina, in the Brightseat formation of Maryland and the lower Hornerstown formation in subsurface sections in New Jersey.

The overlying zone is equivalent to the European Thanetian (or lower Landenian) stage, and to the type Paleocene of the Paris Basin. Elsewhere this faunal assemblage has been termed the "*Globigerina*-keeled *Globorotalia* assemblage," and it is characterized in the region under present discussion by the species *Globorotalia angulata* (White). Other species ranging throughout this *angulata* zone include *Globorotalia aequa* Cushman & Renz, *G. elongata* Glaessner and *G. pseudomenardii* Bolli, as well as the species *G. perclara* and *Globigerina triloculinoides*, which first appeared in the lower Paleocene zone. In addition to these species which range throughout the Thanetian, or middle and upper Paleocene, as here regarded, there are other species of more restricted range, which can be used to delineate subzones. The lowest of these is the *pseudobulloides* subzone, represented by this species which first appeared in the Danian stage and equivalent horizons. *Globorotalia pseudobulloides* is here in association with the first appearance of the above mentioned younger species, that characterize the *angulata* zone. In the relatively complete Alabama section, this subzone is found in the Matthews Landing marl member of the Porters Creek clay and the Coal Bluff marl member of the Naheola formation. Here, in addition to *Globorotalia pseudobulloides* and *Globigerina triloculinoides*, the species *Globorotalia angulata*, *elongata* and *pseudomenardii* all make their appearance in the Matthews Landing, and *G. aequa*, *G. reissi* Loeblich & Tappan and *G. irrorata* Loeblich & Tappan first appear in the Coal Bluff. This zone apparently is not represented in the outcropping section in Texas, but probably appears in the down dip higher subsurface strata. It has not been recognized in the Maryland-Virginia region, but is represented in the subsurface Hornerstown formation of New Jersey.

The upper subzone of the *angulata* zone is termed the *Globorotalia velascoensis* (Cushman) zone in some regions, but that species does not occur in the region under study. The zone is represented here by the very closely related *G. acuta* Toulmin (which occurs with *G. velascoensis* in the Velasco formation and has been regarded as a subspecies by some workers), and by the species *Globigerina spiralis* Bolli, *Globorotalia convexa* Subbotina and *Chiloguembelina crinita* (Glaessner). The older species *Globorotalia pseudobulloides*, *G. compressa*, *G. varianta* (Subbotina), and *Chiloguembelina morsei* and *C. midwayensis* (Cushman) had disappeared by this time. The oldest part of this zone is represented by the upper Hornerstown formation at the outcrop and by the basal Vincentown formation, in which *Globorotalia acuta* has not yet appeared, but which contain *G. angulata* and *G. spiralis*. Possibly an additional subzone could be made for this part of the section, but more detailed zonation must await the availability and study of more nearly complete sections. The typical *velascoensis-acuta* zone also contains *Globorotalia pseudoscitula* Glaessner, *G. occlusa* Loeblich & Tappan and *Globigerina mckannai* White and is represented in the uppermost Velasco formation of Mexico, the upper part of the Lower Lizard Springs formation of Trinidad, the Salt Mountain limestone of Alabama, Aquia formation of Maryland and Vincentown formation (at its type locality) of New Jersey. In addition this zone occurs in beds referred to the Paleocene in the Biarritz seacliffs, the Thanet beds of England (type Thanetian) and equivalent strata in the northern Caucasus of Russia. The Atlantic and Gulf Coast strata here mentioned have in the past been regarded by the U. S. Geological Survey as lower Eocene, but because of their equivalency to the type Thanetian and the Paleocene of France, as well as the greater general resemblance of the planktonic fauna to the older Paleocene zones than to the younger and more diversified Eocene faunas, their Paleocene age cannot be denied.

The lowermost Eocene (Ypresian of Eu-

rope) typically contains a *Globigerina-Globorotalia-Truncorotaloides* assemblage. In the Gulf and Atlantic-coastal region much of the section of this age does not contain planktonic Foraminifera, but the Nanafalia formation of Alabama has an assemblage of 17 planktonic species. A few have persisted from the underlying Paleocene, but the typical Paleocene species such as *Globigerina triloculinoides, G. mckannai* and *G. spiralis, Globorotalia velascoensis, G. acuta, G. angulata, G. occlusa* and *G. pseudoscitula* all have disappeared. The species *Globorotalia rex* Martin, and *G. pseudotopilensis* (Subbotina) are characteristic of this zone, the former being considered as a zone fossil for Ypresian strata. The genus *Truncorotaloides* does not appear in the Nanafalia but is found in more offshore strata of this age.

### CRATACEOUS-TERTIARY TRANSITION TERMINOLOGY AND MICROPALEONTOLOGY

In discussing the Cretaceous-Tertiary boundary formations, care must be taken to utilize the names of the stages, formations, etc., in the sense in which they were defined. For this reason a brief discussion is given here of some of the terms used for late Cretaceous and early Tertiary strata, with reference to their type localities, and certain other occurrences. Comments on their relationships and planktonic assemblages are added.

### EUROPEAN STANDARD STAGES AND AGES

*Maestrichtian.*—The type area of the Maestrichtian is at Maastricht in southern Limburg, Netherlands. It is a tuffaceous chalk with a distinctly Upper Cretaceous megafauna, including ammonites and rudists, *Belemnitella mucronata*, and such vertebrates as *Mosasaurus* and *Plioplatecarpus*. The type Maestrichtian tuffs, Zones Ma (base)–Md (top) are of a facies considerably different from that of other areas. Although containing typical Cretaceous genera, the many species of *Globotruncana, Pseudoguembelina, Racemiguembelina, Planoglobulina, Gublerina* and *Abathomphalus*, characteristic of sediments of late Cretaceous age in other areas, are lacking in this sequence, perhaps because of local environment. The lower part consists of marls with some flints, and the uppermost Maestrichtian (Md) consists of coarse-grained marls with bryozoan beds.

Recently Hofker has made a study of the Foraminifera of the type Maestrichtian, and on that basis has reached some surprising conclusions, stating (1956c, p. 105) that the upper Maestrichtian tuff (Mc and Md) and the Kunrade chalk (regarded by other Netherlands geologists as older than the Maestrichtian tuff) both were younger than type Danian! He also stated (1955b, p. 49) that the Vincentown formation is allied to the Danish Danian as well as to the M-layers of Holland and the Montian, and (1955b, p. 53) "that the *Pseudotextularia*-zone and the upper layers of the Cr 4 are of the same age; that the danish Danian and the Mb are of the same age; that the Kunrade Chalk in its lower layers is of Mb-age; that the Md is younger than the upper zones of the danish Danian; that the outcrop at Vincentown which is considered as Lower Paleocene is older than the Montian of Holland, which likewise is Lower Paleocene." Hofker placed great reliance on the size of pores in certain species, and the occurrence of a number of benthonic species, ignoring rather overwhelming evidence to the contrary, such as the associated Maestrichtian ammonites, belemnites, rudistids, and vertebrates (mososaurs, Cretaceous gener oaf turtles, etc.). In addition, the value of the benthonic Foraminifera is somewhat overrated by Hofker for, as was noted by Bolli (1957), about two-thirds of the benthonic species do cross the Cretaceous-Paleocene contact where complete sections are available for study.

The planktonic Foraminifera also strongly refute Hofker's correlations (his discussion of these in support of this theory, 1956b, notwithstanding). The writers collected a suite of samples from various localities of the Maestrichtian, Kunrade and Gulpens in southern Limburg and nearby Belgium, as well as at their type localities. These samples were collected with the field assistance of three of the Netherlands Survey geologists and Dr. Hofker. The planktonic assemblages we obtained include the following: Upper Gulpens (near Mesch, Netherlands), contained abundant *Rugoglobigerina, Biglobigerinella, Globotruncana*, and *Heterohelix*. The lowest zone of the Maestrichtian (Ma) at the type locality, ENCI

quarry at St. Pietersburg, south of Maastricht, contained *Biglobigerinella* and *Heterohelix;* zone Mb contains abundant *Heterohelix* and *Biglobigerinella* and rare *Rugoglobigerina* and *Globotruncana;* zone Mc contains abundant *Heterohelix* and *Guembelitria*, common *Biglobigerinella* and *Rugoglobigerina* and rare *Globotruncana;* and the base of Md contains *Heterohelix*.

In the Burgerwacht Quarry, St. Pietersburg North, the base of Md contains *Rugoglobigerina* and rare *Heterohelix* and *Guembelitria;* middle Md contains *Heterohelix*, *Guembelitria* and *Biglobigerinella;* and the top of Md contains abundant *Guembelitria* and *Heterohelix* spp., rare *Globotruncana* and poorly preserved *Rugoglobigerina*.

At Chateau Nedercanne, between Maastricht and Eben Emael, Zone Mc contains *Globotruncana, Guembelitria, Heterohelix* spp. and rare *Biglobigerinella*.

In the Biebosch Quarry near Falkenburg, Netherlands, Zone Mb contains *Rugoglobigerina, Heterohelix* and *Biglobigerinella;* Zone Mc contains *Heterohelix* and Zone Md contains *Heterohelix, Guembelitria, Biglobigerinella* and *Rugoglobigina*.

No attempt is made here to identify these forms specifically as it is sufficient to note that the genera *Rugoglobigerina* and *Globotruncana* are restricted to the Cretaceous and the *Guembelitria, Heterohelix* and *Biglobigerinella* are all of Cretaceous types.

Without discussing in detail all of Hofker's reasons for the Tertiary age assignment, a few examples follow:

Hofker originally described the Maestrichtian species of *Biglobigerinella* from the German Upper Cretaceous (*B. biforaminata*) but in Holland considers it Danian. He described *Globotruncana pauperata* from the lower half of the Maestrichtian (Ma–Mb?) (1956a, p. 332), yet considered this horizon Danian. The *Globigerinoides hyalina* Hofker is a malformed Cretaceous *Biglobigerinella*, not the Tertiary genus, as it has two apertural openings of nearly equal size, near the periphery, and does not have an umbilical primary aperture and smaller sutural secondary apertures on the spiral side as does true *Globigerinoides*. He does not recognize the Cretaceous genus *Rugoglobigerina* as distinct from the typical Tertiary *Globigerina*, although the former genus has distinctive apertural cover plates similar to *Globotruncana*, and the latter has a simple open aperture. He records the type species of *Rugoglobigerina, R. rugosa* (Plummer), from the "uppermost Maestrichtian" but below the zones Ma–Md. All species in the "M" zones he considers true *Globigerina*, yet our specimens from each zone at each locality show them to be true *Rugoglobigerina* with cover plates.

In describing *Globorotalia* (*Truncorotalia*) *mosae* from the Maestrichtian Mc–Md, Hofker (1955c, p. 99) stated "Real *Globorotalia* with closed umbilicus and poreless margin without doubt has developed from the last forms of *Globotruncana* with a single keel (Maestrichtian) yet *Truncorotalia* is known only from the lowest Tertiary upward. This species strongly points to the Tertiary age of the Middle Mc and Lower Md." He added that "the species seems to be closely allied to *Globorotalia velascoensis* (Cushman) var. *acuta* Toulmin. . . ." The number of fallacies in these few sentences is outstanding. (1) The type species of *Globorotalia, G. tumida* (Brady) (which is certainly a true *Globorotalia*), does not have a closed umbilicus, but an aperture extending into the open umbilicus. (2) There is a strong doubt that a relatively simple form with an extraumbilical-umbilical aperture developed from a specialized genus such as *Globotruncana* which is characterized by a complex of umbilical plates over a completely umbilical aperture. A far more likely ancestor is the simple *Praeglobotruncana* in the Cretaceous, which grades almost imperceptibly into the characters of the Tertiary *Globorotalia*, or *Globigerina* by a slight apertural extension to an extraumbilical position. (3) *Truncorotalia* was defined as a subgenus of *Globorotalia*, but as their type species have nearly identical characteristics, they are considered synonyms by many paleontologists. Furthermore, Hofker's species is entirely unlike this group of genera and both a specimen sent to us by Hofker and a large suite of topotypes we obtained from personally collected samples show a definite areal aperture in addition to the small, indistinct marginal one. It is a completely unrelated genus, and does not belong to any planktonic family. (4) It is completely unlike *Globorotalia acuta*, in

nearly every feature: the aperture is distinct, as mentioned above, the umbilicus is closed instead of broadly open, the test has a hemispherical section without a prominent and ornamented umbilical shoulder, and the spiral side shows beaded rather than flush sutures. (5) As it is not a planktonic genus and either requires reassignment or perhaps definition of a new genus, it cannot be made the basis for a Tertiary age of the type Maestrichtian.

*Danian.*—The Danian has been commonly regarded in the past as the latest Cretaceous stage. The type locality is at Fakse, Denmark, where the beds have a somewhat specialized fauna, with coccolith and bryozoan chalks and coral limestone facies. The section is incomplete at Fakse as only the middle part of the Danian is exposed. A more nearly complete section occurs at Stevns Klint, some 20 km. from Fakse, where the lower Danian is exposed in contact with the underlying Maestrichtian chalk. Here the basal Danian is a dark colored fish-bearing clay, deposited unconformably in depressions in the eroded white chalk. It is overlain by a *Cerithium* limestone (the *Cerithium baltica* faunal zone), which is in turn followed successively by bryozoan and coral limestones of the *Tylocidaris oedumi*, *T. abildgaardi* and *T. bruennichi* zones (the latter 2 zones being equivalent to the section at Fakse). The youngest Danian zone of *Tylocidaris vexilifera* is not present at either Fakse or Stevns Klint, but is well exposed in a more nearly complete section at Limhamm, near Malmo, Sweden, where all 4 of the *Tylocidaris* zones are found. In the Danian of the Scandinavian region there are no ammonites, no belemnites, and no *Inocerami*, all of which are usually found in Cretaceous strata. The cephalopod group is represented only by "*Nautilus*" *danicus*. Certain of the echinoids, and *Ostrea*, *Crania*, and some other megafossils were said to have a Cretaceous aspect, however.

Bronnimann (1953, p. 339) recorded *Globigerina pseudobulloides* Plummer, *Globigerina daubjergensis* Bronnimann, and *Globorotalia compressa* (Plummer) from the type Danian of Denmark, Troelsen (*in* McLean, 1955) also recorded *Globigerina triloculinoides* Plummer from the Danian. The present writers (Loeblich & Tappan, 1957) have recently recorded the following planktonic species of Foraminifera from the type Danian: *Globorotalia compressa* (Plummer), *Globorotalia pseudobulloides* (Plummer), *Globigerina triloculinoides* Plummer, *Chiloguembelina morsei* (Kline) and *Globigerinoides daubjergensis* (Bronnimann). All but the last named were described originally from lower Midway strata of the Gulf Coast; the *Globigerinoides* having been described originally from the Danian of Denmark but obtained by the writers also in the upper Danian of Sweden and the following formations of the Midway group of the Gulf Coast: Kincaid and Wills Point formations of Texas and the Pine Barren and McBryde members of the Clayton formation in Alabama. It also occurs in the Paleocene Brightseat formation of Maryland and in the lower part of the Hornerstown formation of New Jersey. This entire assemblage is typical of lower Paleocene, Danian and lower Midway strata, regardless of the term which had been previously applied to the strata. It occurs in the type Danian with a large amount of reworked Cretaceous material. The type "Danian" therefore represents a local lithologic and faunal facies of the lower Paleocene, the presence of the above-mentioned Paleocene planktonic foraminiferal fauna showing that it is equivalent to the lower Midway in age. The Danian is unconformably overlain by the Seelandian Tertiary clays. This "typical" Danian facies is not present elsewhere in Europe as the Danian in general was a time of regression of the sea and in many places is represented by nonmarine deposits or is missing completely.

Cuvillier et al. (1955) noted the Danian *Globigerina* zone in the flysch of the southern occidental Aquitaine basin, and in the Aturian limestones of the north occidental Aquitaine, at Tercis, Audignon, etc., occurring below the typical *Globorotalia* fauna of the Paleocene. At each locality he noted the contrast between "le Danien à affinités éocenès" containing numerous globigerinids, and the underlying Cretaceous with *Globotruncana*. He placed the Danian-Paleocene contact at the base of the *Globorotalia* zone.

The present writers in 1954 collected a series of samples in the Biarritz seacliffs,

where below the well-known Eocene blue marls were sediments identified as Danian and Paleocene in age. Examination of their planktonic assemblages showed that in the Falaise de Casaville, the lower part of the Danian reddish marly beds between harder layers, which parallel the underlying hard grey or brown Cretaceous marls contain a Danian "*Globigerina*" assemblage. The higher beds in this outcrop represent the early part of the *Globigerina*-keeled *Globorotalia* assemblage. Nearby in the same cliff but somewhat farther north, the "Paleocene" beds (as identified by the French) contain a younger *Globigerina*-keeled *Globorotalia* assemblage.

The lowest sample obtained of the Danian at Biarritz contains *Globigerinoides daubjergensis*, *Chiloguembelina midwayensis*, *Globorotalia compressa*, *G. pseudobulloides* and *Globigerina triloculinoides*, and thus correlates with the lower Midway group, type Danian, and beds of equivalent age.

A sample of similar lithology, about 20 feet higher in the section, contained *Chiloguembelina midwayensis*, *Globigerina triloculinoides*, and *Globorotalia pseudobulloides*, *G. elongata* and *G.* cf. *G. angulata*. This is a distinctly younger assemblage, belonging to the *pseudobulloides* subzone of the *angulata* zone, of the lower Thanetian, as shown by the coexistence of *G. pseudobulloides* and *G. angulata* and *G. elongata*. It is thus equivalent to the Porters Creek clay and Naheola formation of Alabama, and subsurface Hornerstown formation of New Jersey.

The "Paleocene" beds at Biarritz contain a more varied fauna of planktonic species, representing the *velascoensis-acuta-spiralis* subzone of the *angulata* zone, and equivalent to the upper Thanetian. It contains all of these zone species, *Globorotalia* cf. *G. angulata*, *G. velascoensis*, *G. acuta* and *Globigerina spiralis*, in addition to *Globigerina inaequispira* Subbotina and *G. mckannai*. *Chiloguembelina* cf. *C. crinita*, *Globorotalia pseudomenardii*, *G.* cf. *G. aequa* and *G. occlusa*. These species relate the Biarritz "Paleocene" exactly to the upper Velasco formation of Mexico, upper zone of the lower Lizard Springs formation of Trinidad, the Salt Mountain limestone of Alabama, Aquia formation of Maryland and Vincentown formation of New Jersey, and a similar zone in the Russian Caucasus.

In the northern Apennines of Italy, Cita (1955) reported the Upper Maestrichtian with the typical "*Globotruncana-Pseudotextularia-Guembelina*" assemblage. The overlying unit, containing a fauna of "*Globigerina*," "*Globigerinella*" and "*Guembelina*" was considered to be Danian. The third recognizable fauna was referred to the Paleocene, and marked by the disappearance of "*Globigerinella*" and "*Guembelina*" and the appearance of *Globorotalia* (including *G. velascoensis*). The fourth unit was similar but contained additional species of *Globorotalia*, *Globigerina*, *Hantkenina*, and *Globigerinoides mexicanus* (Cushman), and was referred to a middle Eocene age. Cita noted that in some areas one or more of these units might be absent but without any apparent unconformity, suggesting perhaps either a hiatus in sedimentation or the effect of submarine erosion.

In the Petites Pyrenees of France, the Middle Garumnian has been correlated with the Danian, but Garumnian here consists of nonmarine lacustrine limestones, and is correlated solely on the basis of stratigraphic position, as it overlies the Maestrichtian and underlies beds (upper Garumnian) identified as Montian on the basis of *Cerithium inopinatum*.

We do not necessarily imply that all beds referred to the Garumnian or Danian are of Paleocene age. For example, strata referred to the Garumnian at Isona, province of Lerida, Spain, have been correlated with the Danian. The writers visited this locality in 1954 with Dr. J. R. Bataller of Barcelona, and found the strata to contain rudistids, and to be of late Cretaceous age, neither correlative with the Danian nor the Paleocene.

Reichel (1953, p. 347) believed that *Globorotalia* is absent throughout boreal Europe, and that therefore in the type Danian there could be no boundary apparent between the *Globigerina* and the *Globigerina-Globorotalia* zones. Although *Globorotalia* may be less abundant in boreal areas than in the Tethys region, the reported occurrence in the Thanet beds of England is from a boreal area. Furthermore, Cushman

(1915, p. 55) recorded living *Globorotalia menardii* (d'Orbigny) as "not uncommon in the North Pacific," and *G. truncatulinoides* (d'Orbigny) (p. 59) as "one of the most common species of the North Pacific."

The absence of angular *Globorotalia* in the type Danian is undoubtedly because of its nonexistence in beds of that age, the upper Paleocene not being there represented, for the species found in the Danian are those found throughout the world only in the lower faunal zones of the Paleocene, and not those typically associated with the keeled *Globorotalia* fauna. At the fourth World Petroleum Congress, many European micropaleontologists reported the same sequence of planktonic Foraminifera in the Cretaceous-Tertiary boundary strata, in Italy, the French Aquitaine basin, Tunisia, Morocco, Libya, Syria, and Algeria, it has been reported previously in Palestine, Egypt, Sweden, the Lizard Springs of Trinidad, Velasco of Mexico and Midway of Texas, and we have observed it also in the Midway group of Alabama, the Biarritz area of France, the Brightseat-Aquia formations of Maryland, and in the Hornerstown-Vincentown section of New Jersey. Certainly the absence of keeled-*Globorotalia* in the lower Midway of Alabama, Texas, Trinidad and México, is not due to a boreal environment.

*Paleocene.*—The term Paleocene is not always used in Europe, although it was first defined there. Schimper introduced the term in 1874 to include the Bracheux sands and the lignitic beds of Soissons, in the Paris Basin. The term was proposed because the fauna and flora of those strata retain some archaic characteristics which disappear at their close, although the aspect as a whole is like the Cenozoic. To date, the Foraminifera of this type Paleocene section of the Paris Basin have not been described. Samples of the Bracheux sands collected by the writers did not contain planktonic species, probably because of the near shore depositional environment. The lignites of Soissons are nonmarine. Paleocene beds in the Biarritz area are of Thanetian age. We propose enlarging the scope of the term Paleocene, to include both the Danian and Thanetian stages, because of their close faunal relationship. It has previously been used to include the Montian and Thanetian or Montian and Landenian stages, but as shown below the Montian and Danian are synonymous.

*Montian.*—Avoiding the use of the term Paleocene, some European geologists use the stage names Montian and Landenian within "Lower Eocene." Others use them as subdivisions of the Paleocene.

The Montian was described from Mons, Belgium, where it occurs as local deposits in the eroded surface of the chalks. It is considered to represent a transgressive stage, appearing in the central regions of Europe, which have no "Danian" deposits. A decidedly Tertiary-appearing fauna of *Cerithium* and *Turritella* occurs in the soft limes, and wherever this distinctive gastropod fauna is found the Montian has been recognized. As mentioned above, the Danskekalk formation (type Danian of Denmark) also has a "*Cerithium* limestone" as its basal member. This basal Danian *Cerithium* represents a distinct species and thus is not an indication in itself of exact time equivalency, but it nevertheless represents a facies similar to that of the type Montian. Material from the Tuffeau de Ciply (lower part of the type Montian) was sent to us by Dr. John Troelsen of Copenhagen, Denmark and contains the following planktonic species: *Globigerinoides daubjergensis* and *Globigerina triloculinoides*.

The occurrence of the *Cerithium* fauna in the type Danian, and *Nautilus danicus* in Montian equivalents, the species of the *daubjergensis-compressa* faunal zone represented in both type Danian and type Montian and their equivalents over the world, the identical stratigraphic position of the Danian and Montian, each unconformable on the Cretaceous, and underlying the Landenian sediments, and the fact that they are never found together, leads inescapably to the conclusion that the Danian and Montian are merely different lithologic and faunal facies of identical geologic age. We suggest that the term Danian be used to include the Montain also, inasmuch as the type Danian includes beds of both facies. The Danian should be used as a stage name within the Paleocene.

The Montian equivalent in the Paris Basin is the "calcaire pisolithique." At Vigny it consists of a *Lithothamnium* reef, formed at the base of the ancient Cretaceous chalk cliffs. The position adjacent to the Cretaceous chalk in quarries had led to the belief for some years that the "calcaire pisolithique" was merely a lateral facies of the Cretaceous chalk, and in fact *Belemnitella* had been reported from it. The definitely Tertiary microfauna of the "pisolithique" recorded by Marie (1937), the occasional fragments of the chalk (and reworked *Belemnitella*) found embedded in the "calcaire pisolithique," and the absence of fragments of the calcaire in the Cretaceous, as well as weathering of the chalks at their contact, and the limited occurrence of the reefal deposits, finally led to the conclusion that the "calcaire pisolithique" was stratigraphically younger, and equivalent to the Montian of Belgium. Later de Lapparent (1939) noted the presence of *Nautilus danicus* in the "calcaire pisolithique" at Vigny, and commented that it had been observed before in Montian deposits. Lemoine (1937) in discussing the "calcaire pisolithique" stated that one could not decide in the Paris basin alone whether or not the Danian and Montian were synonymous, but recommended that it be considered a single stage, Danian-Montian.

*Thanetian.*—The type locality of the Thanetian stage (Thanet beds) is in England, where it consists of a marine glauconitic sand with *Cyprina* and *Cucullaea*, another near shore facies distinct from those previously mentioned. There is some disagreement as to whether Thanetian should be used as a substage or as a stage. It is regarded by some as equivalent to the Landenian, and by others as the lower substage of the Landenian, followed by the Sparnacian. This problem was discussed by Haynes (1955, p. 189). In England the marine Thanet beds and the overlying nonmarine Woolwich and Reading beds are regarded as deposits of the same sedimentary cycle. A similar sequence occurs in the Paris Basin type Paleocene where the Sables de Bracheux (equivalent to Thanetian) is followed by the Lignites du Soissons (similar to the Woolwich and Reading beds). The latter nonmarine strata are generally referred to the Sparnacian.

Samples from the Thanet beds were collected by the writers from Herne Bay and Pegwell Bay, Kent County, England, where they consist of sandy and shelly strata. In these samples we found no planktonic species. Haynes (1955, p. 189) studied Thanet material from sandy silts exposed in the cliffs at Reculver, and found them to contain *Globigerina triloculinoides* Plummer, *Globigerina pseudobulloides* Plummer, and *Globorotalia wilcoxensis* var. *acuta* Toulmin, showing the presence of the highest Paleocene planktonic faunal zone—the *Globorotalia velascoensis-acuta* zone.

*Sparnacian.*—The Sparnacian (with type locality at Epernay, northeast of Paris) follows the Thanetian substage in the European time-scale. It is a nonmarine facies, with clays and lignites, with a few intercalated marine shelly beds. It may be in part equivalent to the Thanet beds and in part younger (the English equivalents are the Woolwich and Reading beds, nonmarine strata overlying the Thanet). Some authors consider the Sparnacian as basal Eocene rather than Paleocene, but at least in England the nonmarine beds and the underlying marine ones are regarded as belonging to the same depositional cycle. The fauna suggesting the *velascoensis-acuta* planktonic faunal zone, reported by Haynes (1955) from the Thanet beds, is the youngest Paleocene faunal zone yet identified, and is elsewhere followed by Lower Eocene strata. Until marine strata referable to the Sparnacian can be obtained this problem is difficult to solve. It may represent both late Paleocene and early Eocene time.

### PALEOCENE IN NORTH AFRICA AND THE MIDDLE EAST

Many recent publications have demonstrated the presence of a locally rather complete Paleocene sequence, in Egypt, Algeria, Libya and Syria, Tunisia, and Palestine.

Tromp (1949, p. 675) stated that the term Danian was widely used where there was difficulty in distinguishing the Cretaceous-Eocene boundary. As the microfossils supply very accurate evidence for this bound-

ary, he considered that the term should be eliminated in the Middle East, Germany, Italy and Morocco, where the boundary had been determined. With further micropaleontologic studies "The Danian would probably prove to be a superfluous unit that has been useful only because of the great difficulty experienced in determining the Cretaceous-Eocene boundary by means of macro-fossils."

Nakkady (1951, 1955) studied the chalk and overlying Esna shale of Egypt and established three biozones in the Mesozoic-Cenozoic transition beds, based on planktonic Foraminifera: a *Globotruncana* zone of Campanian-Maestrichtian age at the base, a Buffer zone (the *Globigerina* zone), of Danian age, distinguished by the complete absence or extreme scarcity of both *Globotruncana* and angular species of *Globorotalia*, and at the top a *Globorotalia* zone of Dano-Paleocene age. This faunal sequence has since been observed in many areas throughout the world. The Esna shale is a lithologic facies, in some regions including beds ranging from Maestrichtian to upper Paleocene age, but in other localities only the middle part of this section may be represented as shale and the lower and uppermost shales are replaced by contemporaneous chalk deposits. Nakkady therefore recommended the use of faunal zones in place of the lithologic terms in Egypt.

The variable occurrence of the Danian sequence suggests rather widespread tectonic movements at the close of the Mesozoic, and many areas show physical evidence of a break in sedimentation between the Cretaceous and Paleocene, in addition to a pronounced faunal change. In other areas, continuous deposition has been reported from the Cretaceous to the Eocene. In many of these, later detailed work has brought forth evidence of a formerly unsuspected hiatus. Nakkady (1949, p. 246) noted that in the Oasis of Farafra, Egypt, many authors from the time of Zittel considered the two systems to be perfectly conformable. He listed as supporting evidence: 1) about one-third of the Esna shale fauna appeared first in the Cretaceous, about one-third of the fauna continued into the Eocene, 2) the absence of any visible lithologic break, and 3) the stratigraphic position of the Esna shales. He considered the Esna shales thus to be "Passage-beds between the Cretaceous and Eocene."

However, as noted by Bolli and others, many benthonic species do cross the Cretaceous-Paleocene boundary even in areas where a disconformity or unconformity is known to be present. In other areas where an unconformity is not visibly apparent, it has been proved to exist by faunal gaps, electric logging methods, etc. Possibly the application of additional methods may yet prove the existence of such an unconformity in the Farafra Oasis area as well as in the other localities in Egypt, where the Danian is extremely variable in extent and thickness.

Reiss (1955) discussed the Cretaceous-Tertiary boundary in Israel, and the micropaleontologic evidence for its determination. In this region the Maestrichtian contains the typical Cretaceous "*Guembelina-Globotruncana*" microfauna. Above this in Israel also is a *Globigerina* zone devoid of both *Globotruncana* and angular *Globorotalia* (considered by Reiss to be Danian), which in turn is overlain by a *Globigerina-Globorotalia* zone (which Reiss termed the Paleocene). He stated that there is everywhere a sharp faunal change at the Maestrichtian-Danian boundary, representing a time lapse and an extensive unconformity caused by tectonic movements. This he considered to be the Cretaceous-Tertiary boundary, and he stated that deposits containing true "transitional" Maestrichtian-Danian faunas are unknown as yet, although they may eventually be discovered in deep sea deposits. He correlated the lower Midway group with the Danian (*Globigerina* zone) and the upper Midway group of Texas and lower Velasco shale of Mexico with the Paleocene, as they included the *Globigerina-Globorotalia* zone. He thus considered the Danian as belonging to the Tertiary, suggesting that perhaps a new series (epoch) of the Tertiary should be created to include both Danian and Paleocene.

In Libya and Syria, Lys & Renouard (*in* Cuvillier et al., 1955), noted the abrupt faunal change from the Cretaceous *Globotruncana* zone to that of the *Globorotalia-*

bearing Paleocene, and stated that the evident reworking of *Globotruncana* and *Guembelina*, and the oxidation of the sediments suggest an uplift and possible emersion, resulting in the absence in this region of the Danian *Globigerina* faunal zone.

Magné & Sigal (*in* Cuvillier et al., 1955) also recognized the *Globotruncana* zone followed by the *Globigerina* zone and finally the angular *Globorotalia* assemblage, in Algeria.

Dalbiez & Glintzboeckel (*in* Cuvillier et al., 1955, p. 532–533) noted the same sequence in Tunisia, for in the northwest part, there were the typical three planktonic faunas of Cretaceous, Danian and Paleocene. In the eastern region the middle (Danian) zone of *Globigerina* is absent, and the keeled *Globorotalia* faunal zone rests in apparent conformity on the *Globotruncana* beds. A detailed lithologic examination, and evidence of reworked Maestrichtian species in the overlying zone led to the supposition of a lapse in the sedimentation, although perhaps without real emersion.

Said & Kenawy (1956) described the Upper Cretaceous and lower Tertiary Foraminifera from northern Sinai in Egypt, but in contrast to earlier workers, placed greater emphasis on the benthonic Foraminifera as age indicators. They cited Todd (1954) who had considered planktonic species limited to the open-sea facies and thus of limited availability. Said & Kenawy added that "this makes the use of planktonic species of rather limited value." In addition to agreeing with Todd that the planktonic species might be "facies-controlled," they then disregarded their value as time indicators as well, and (1956, p. 114) "abandoned the classic and oft-repeated zoning based on the planktonic Foraminifera *Globigerina* and *Truncorotalia*. We feel that these forms are facies fossils, which may have some zoning value but which occur, like their descendants in modern times, only in open and moderately deep seas." They therefore assume that the first occurrence of *Truncorotalia* in Egypt cuts across time lines, wherever it does not agree with the upper limits of the species *Bolivinoides delicatula* Cushman and *Neoflabellina jarvisi* (Cushman). After stressing the rapid facies changes in the Egyptian section, with considerable emphasis on the overlap, offlap, etc., Said & Kenawy place more reliance on the benthonic species for time zonation than on the planktonic *Truncorotalia* (=*Globorotalia*) and refer to the "*Neoflabellina jarvisi* time surface" and the "*Bolivinoides delicatula* time surface."

This statement seems to be contradicted in the diagram given by Said & Kenawy (1956, p. 155) in which the "*Bolivinoides delicatula* time surface" lies at the contact between shale ("Danian") and shaly limestone ("Paleocene") and the "*Neoflabellina jarvisi* time surface" lies at the contact between the shaly limestone and the overlying limestone with flint. In their diagram the "*Truncorotalia*" (=keeled *Globorotalia*) surface crosses all of these lithologic zones, hence does not seem to be very strongly "facies-controlled."

Although we do not minimize the value of the benthonic species in correlations and age determination, the planktonic species are certainly no more "facies-controlled."

Said & Kenawy (1956), although deprecating the value of *Globorotalia* did admit that the Cretaceous planktonics were of value, and used the *Globotruncana-Guembelina* (=*Heterohelix*) boundary as a time indicator in comparing their sections to those of earlier workers in Egypt. As *Globorotalia* and the other Tertiary planktonic genera have proved valuable for detailed correlation over such distant points as Russia, England, France, the United States, México and Trinidad, it seems probable that the Egyptian sections of "retarded *Truncorotalia*" (the *Globigerina*-keeled *Globorotalia* assemblage) merely are sections of greater thickness of the Danian, beneath the upper Paleocene. In sections where angular *Globorotalia* appear immediately above the Cretaceous *Globotruncana* zone, it is an indication of an underlying unconformity or disconformity.

## PALEOCENE IN RUSSIA

The zonation and foraminiferal succession in Russia, as given by Subbotina (1953) is very similar to that found elsewhere, except that the Paleocene-lower Eocene boundary is placed at the lower rather than the upper limit of the *Globorotalia velascoensis* zone.

Species which are common to Russia and to the American Gulf and Atlantic Coast were discussed by Loeblich & Tappan

(1957). They record the Russian species *Chiloguembelina crinita* (Glaessner), *Globigerina inaequispira* Subbotina, *Globorotalia convexa* Subbotina and *G. elongata* Glaessner all from the Velasco shale of México, the Hornerstown and Vincentown formations of New Jersey, the Aquia formation of Maryland and the Salt Mountain limestone and Nanafalia formation of Alabama. *Globorotalia imitata* Subbotina and *G. varianta* (Subbotina) occur in the Wills Point formation of Texas and the Matthews Landing marl member of the Porters Creek clay of Alabama and the former also in the Velasco shale of México, Aquia formation of Maryland, Vincentown formation of New Jersey and Nanafalia formation of Alabama. *Globorotalia pseudotopilensis* (Subbotina) occurs in the Nanafalia formation of Alabama and *G. pseudoscitula* Glaessner occurs in the Velasco shale of México, the Coal Bluff marl member of the Naheola formation and the Salt Mountain limestone of Alabama, the Aquia formation of Maryland, and Vincentown formation of New Jersey. *Globigerina triloculinoides* Plummer was originally described from the Midway group of Texas and reported by Subbotina from Russia. It occurs in all the above-mentioned American Gulf and Atlantic Coast Paleocene formations as well as in the Brightseat formation of Maryland and the McBryde limestone member of the Clayton formation of Alabama. *Globorotalia compressa* (Plummer) appears to be recorded in Russia as *Globorotalia membranacea* (Ehrenberg) and occurs in this hemisphere in the Velasco shale of México, Wills Point formation of Texas, McBryde limestone member of the Clayton formation and the Brightseat formation of Maryland. Both *Globigerina triloculinoides* and *Globorotalia compressa* also occur in the Danian in Scandinavia.

*Globorotalia velascoensis* (Cushman), originally described from México, also was reported in Russia by Subbotina (1953).

Detailed zonation and range charts based on the planktonic species were given by Subbotina (1953) and show a general similarity to the Gulf Coast succession. Unfortunately, the as yet insurmountable obstacles in obtaining comparative material from Russia have made it impossible in some cases to know whether forms described under different names in Russia and elsewhere are in reality identical. In general, the descriptions and illustrations are sufficiently good that we have been able to use many of the Russian names with reasonable certainty of their identity. The lowest zone reported in the Caucasus contains *Globorotalia pseudoscitula, G. compressa, G. pseudobulloides, G. varianta, G. imitata* and *Globigerina triloculinoides*, all of which are found in the other regions of Paleocene deposits here discussed together with a few other Russian species of *Globigerina* and *Globorotalia*. This zone is regarded by Subbotina as Danian, but seems possibly referable to our *pseudobulloides* subzone, *angulata* zone, or lower Thanetian stage.

The strata referred by Subbotina to "Paleocene-lower Eocene" contains *Globorotalia pseudotopilensis, G. varianta, G. pseudoscitula* and *Globigerina triloculinoides*. Above this is a zone containing *Globorotalia velascoensis, G. pseudoscitula, G. aragonensis, G. pseudotopilensis, Globigerina triloculinoides* and *G. inaequispira*. Subbotina termed this part of the section, middle to upper Eocene, but the species show that it is equivalent to the late Paleocene and early Eocene as these are elsewhere identified. Although the age assignments differ somewhat, and some specific identifications remain doubtful it is interesting to note the generally similar sequence of planktonic species.

### PALEOCENE IN MÉXICO AND THE CARIBBEAN

*Velasco formation.*—The Velasco formation of the Tampico embayment of México was first separated from the Upper Cretaceous Mendez formation by Cushman & Trager (1924), and was then thought to be related to the Taylor marl of Texas. Later, Cushman (1926) stated it to be equivalent to the Navarro of Texas. Dumble & Applin (1924) described the same sequence of beds as the Tamesí formation and considered it to be lower Eocene. At least locally the Velasco formation rests unconformably on the Upper Cretaceous Mendez formation, and the basal Velasco was collected just above this unconformity in Borrega Canyon, Tamaulipas, México, by A. R. Loeblich, Jr.

The faunal lists given by Muir (1936, p.

81) for the basal Velasco (Tamesí), which had been prepared by Helen Jeanne Plummer contain only *Globigerina* and nonkeeled *Globorotalia* suggestive of the lowest faunal zone here described. The *Globigerina*-keeled *Globorotalia* fauna occurs in the middle and upper Velasco, like that of the upper Paleocene elsewhere.

*Globorotalia velascoensis* (Cushman), *G. angulata* White and *Globigerina mckannai* White were originally described from the Velasco shale of México. Because of its worldwide geographic and restricted geologic occurrence *G. velascoensis* is considered to be a zone fossil for latest Paleocene (Bolli, 1957; Loeblich & Tappan, 1957).

A sample of the upper part of the Velasco shale in Tamaulipas was found to contain the following species (described and illustrated by Loeblich & Tappan, 1957): *Chiloguembelina crinita* (Glaessner), *Globigerina mckannai* White, *G. triloculinoides* Plummer, *G. inaequispira* Subbotina, *Globorotalia pseudomenardii* Bolli, *G. elongata* Glaessner, *G. imitata* Subbotina, *G. convexa* Subbotina, *G. troelseni* Loeblich & Tappan, *G. pseudoscitula* Glaessner, *G. velascoensis* (Cushman), *G. aequa* Cushman & Renz, *G. angulata* (White) and *G. occlusa* Loeblich & Tappan, all of which occur in late Paleocene strata elsewhere.

*Lizard Springs formation.*—Exhaustive studies of the planktonic Foraminifera of the Lizard Springs formation of Trinidad, B.W.I., have made possible a detailed zonation (Bolli, 1957). Bolli recognized five planktonic zones in the lower Lizard Springs. The lowest contains the species *Globigerinoides daubjergensis, Globigerina triloculinoides, Globorotalia pseudobulloides* and *G. compressa*, which are representative of the *daubjergensis-compressa* zone as defined by Loeblich & Tappan (1957). His second and third zones are probably equivalent to our *pseudobulloides* subzone of the *angulata* zone, containing in common with our material the species *Globigerina triloculinoides, G. spiralis, Globorotalia compressa, G. pseudobulloides* and *G. angulata*. His upper two zones both contain *Globorotalia velascoensis*, and in addition the species *G. pseudomenardii, G. aequa, G. elongata* and *Globigerina mckannai*, also indicative of our highest planktonic faunal zone in the Paleocene. The upper Lizard Springs formation is of Eocene age, and Bolli erected three planktonic faunal zones in the Eocene. The lowest he named the *Globorotalia rex* zone, and the same species is used by us as representative of this age where it occurs, as in the Nanafalia formation of Alabama. His higher zones do not occur in the formations studied for the present paper.

### PALEOCENE AND LOWEST EOCENE IN THE ATLANTIC AND GULF COASTAL PLAIN

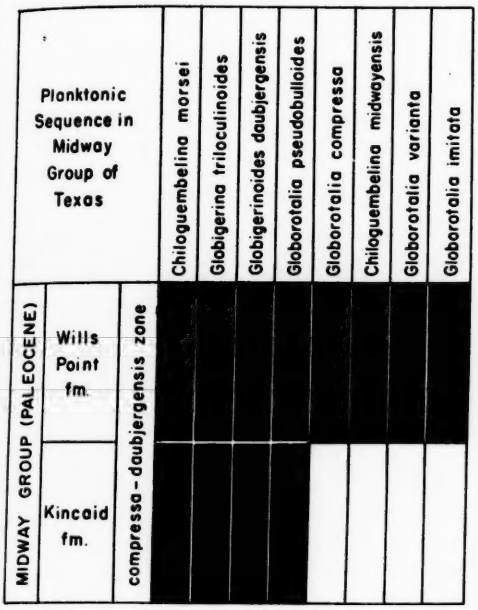
*Midway group.*—The Midway group was originally described from Alabama, and since 1894 has been recognized generally as including the oldest Tertiary beds of the Gulf Coastal Plain. It was long considered by the U. S. Geological Survey to be lower Eocene in age (Wilmarth, 1938, p. 1366). However, about 30 years ago, Gayle Scott (1926, p. 161) correlated the Midway group of the Gulf Coast with the Danian, placing the nautiloid *Enclimatoceras ulrichi* White into the synonymy of *Hercoglossa danica* (Schlotheim). He considered (1934, p. 1158) that the Midway was therefore of Cretaceous age, as the Danian was generally regarded as late Cretaceous.

Gardner (1933, p. 92) first placed the Midway group in the Paleocene, the lower Midway (Kincaid) being considered Montian, and the upper Midway (Wills Point) correlated with the Landenian. She stated (p. 99) that "The existence of marine deposits of Danian age in either of the Americas has not been established."

Brotzen (1948, p. 32) placed the Kincaid in the Danian, Wills Point in Seelandian, and the lower Wilcox was considered equivalent to the Thanetian and younger.

This disagreement is more apparent than real, however, for as was mentioned above, the type Montian and type Danian are of equivalent age, and belong to the Lower Paleocene. Gardner (1933) was correct in considering the Midway equivalent to the Montian, and Scott (1926) was also correct in assigning to it a Danian age. Scott erred only in considering it as late Cretaceous.

Samples examined for the present study from Midway strata in Texas (Text-fig. 3) included some from the Pisgah member of the Kincaid, from strata regarded by Plummer as transitional between the Kincaid




TEXT-FIG. 3

and Wills Point, from the Mexia clay (lower part of the Wills Point formation) and other localities of uppermost Wills Point, from Freestone, Limestonè and Navarro counties of Texas. The planktonic fauna of the Kincaid and Wills Point was similar, the Kincaid containing *Globigerinoides daubjergensis*, *Globigerina triloculinoides*, *Globorotalia pseudobulloides* and *Chiloguembelina morsei*, indicative of the *daubjergensis-compressa* faunal zone of lowest Paleocene (Danian) age.

The Wills Point formation contains all of the above species, and in addition *Globorotalia compressa*, *G. imitata*, *G. varianta* and *Chiloguembelina midwayensis*. Although slightly more varied, this fauna is still indicative of the lowest Paleocene, and is pre-Thanetian, lacking the angular *Globorotalia* of the middle and late Paleocene.

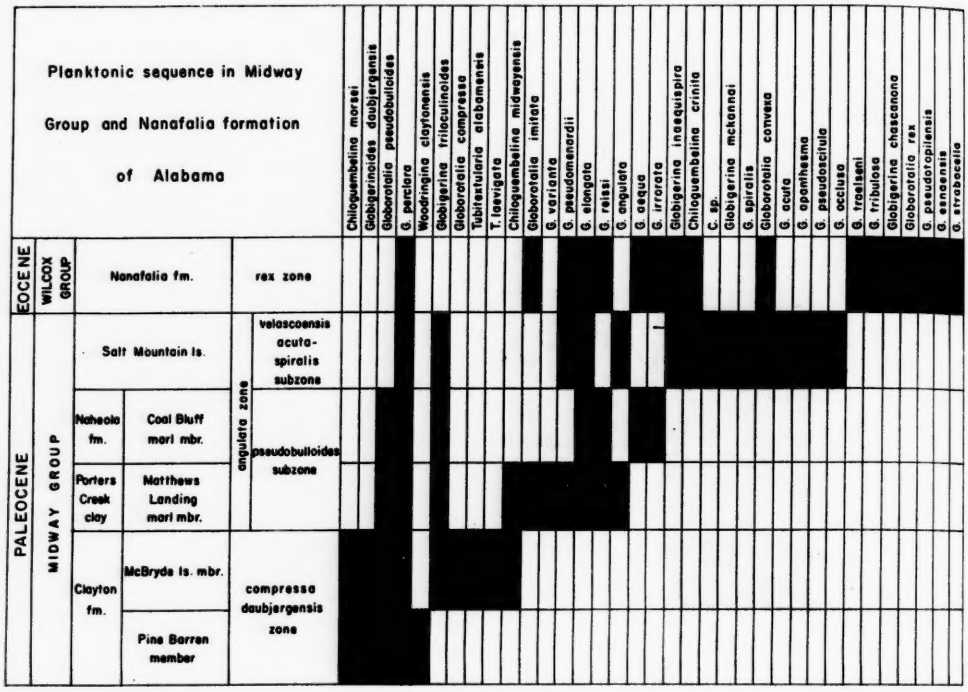
Younger Midway strata have been reported from the subsurface in Texas, however.

The Midway section in Alabama is more nearly complete (Text-fig. 4). For this study, samples were obtained from Wilcox, Choctaw and Sumter counties, Alabama, from the Pine Barren and McBryde members of the Clayton formation, the Porters Creek clay and the Matthews Landing marl member of the Porters Creek clay, and the Oak Hill member and Coal Bluff marl member of the Naheola formation, all of which are regarded generally as comprising the Midway group in Alabama. Samples of the Salt Mountain limestone in Clarke County, and of the Nanafalia formation in Wilcox and Marengo counties, both regarded as belonging to the Wilcox group by the U. S. Geological Survey were also studied. These formations are discussed under separate headings below, but their planktonic faunas clearly show that the Salt Mountain limestone should be referred to the Midway group, whereas the fauna of the Nanafalia is of a distinctly younger appearance, and typical of Wilcox (Ypresian) age.

An excellent planktonic zonation can be developed in the above mentioned sequence, even though the Porters Creek clay and the Oak Hill member of the Naheola formation contained no planktonic species in the samples examined. The remaining formations represent all of the Paleocene faunal zones previously erected and discussed above.

The Pine Barren member contains *Globigerinoides daubjergensis*, *Globorotalia pseudobulloides*, *G. perclara*, *Chiloguembelina morsei* and *Woodringina claytonensis* and thus is equivalent in age to the lower part of the *daubjergensis-compressa* faunal zone, the type Danian and the Kincaid formation of Texas. The McBryde limestone member contains all of the above mentioned species with the exception of *Woodringina* and in addition *Globigerina triloculinoides*, *Globorotalia compressa*, *Chiloguembelina midwayensis*, *Tubitextularia alabamansis* Cushman and *T. laevigata* Loeblich & Tappan. This slightly more varied fauna represents the upper part of the *daubjergensis-compressa* zone and is equivalent to the Wills Point formation of Texas.

The Matthews Landing and Coal Bluff marl members show a fauna representing the lowest (*pseudobulloides*) subzone of the *angulata* zone or lowest Thanetian, and are characterized by numerous species of angular *Globorotalia*. In addition to the zonal markers *Globorotalia angulata* and *G. pseudobulloides* the Matthews Landing also rep-




TEXT-FIG. 4

resents the first appearance of *G. elongata*, *G. pseudomenardii*, *G. reissi*, in association with species continuing from the lower zones, *G. imitata*, *G. perclara* and *G. varianta*, *Globigerina triloculinoides* and *Chiloguembelina midwayensis*. In the Coal Bluff member, the fauna is quite similar but did not contain *Globorotalia angulata*, *G. imitata*, *G. pseudomenardii* or *G. varianta*. All but the last of these are found in higher as well as lower zones, hence will probably be found with study of additional material of the Coal Bluff. This formation also lacks *Chiloguembelina midwayensis* which made its last appearance in the Matthews Landing. Although regarded by the U. S. Geological Survey as the youngest part of the Midway group in Alabama, this zone is only of middle Paleocene age, as recognized elsewhere. The upper Paleocene zones do appear in Alabama, in the Salt Mountain limestone, and because of the Paleocene age, the writers recommend the inclusion of the Salt Mountain limestone within the Midway group of Alabama, as its youngest formation. It is discussed more thoroughly below.

*Salt Mountain limestone.*—The Salt Mountain limestone of Alabama is recognized by the U. S. Geological Survey to be of lower Eocene age and to belong to the Wilcox group (Wilmarth, 1938, p. 1898). The only known outcrops are at Salt Mountain and in its immediate vicinity. It has been regarded as lying between the Nanafalia formation and the Tuscahoma sand, although it does not appear in contact with these formations. Originally regarded as Oligocene because of its position adjacent to other Oligocene strata, later study proved that the present occurrence of the Salt Mountain limestone at its type locality is due to its being upthrust by the Jackson fault (Cooke, 1935, p. 1164). Vaughan (1936) described two species of *Discocyclina* from the Salt Mountain limestone, *D. blanpiedi* and *D. cookei*, regarding them as of lower Eocene age. Small specimens of *D. blanpiedi* also occur in material from the Coal Bluff marl member, which is regarded

as Paleocene by the U. S. Geological Survey.

Toulmin (1941, p. 569) recorded 99 species of Foraminifera from the Salt Mountain, of which 19 were common to the upper Wilcox greensand at Ozark, Alabama; 10 occurred in the upper Wilcox (Bashi) of Woods Bluff, Alabama; 11 occurred in the lower Midway (Kincaid) of Texas; 18 were found in the upper Midway of Texas, and 14 were found to occur in a Midway fauna in Alabama.

Over 20 per cent of the Salt Mountain foraminiferal species are present in the Vincentown formation of New Jersey. Thus, on the basis of the total fauna, the Salt Mountain has about the same number of species in common with the Midway elsewhere (18) as it does with the Wilcox group (19). Toulmin considered that at least the upper part was younger than Midway and probably of early Wilcox age (Eocene).

The planktonic species nevertheless show a much closer affinity to the Paleocene than to the Eocene for Toulmin recorded *Globigerina compressa* Plummer, *G. triloculinoides* Plummer, *Globorotalia membranacea* (Ehrenberg) [=*G. pseudomenardii* Bolli] and *G. wilcoxensis* Cushman & Ponton var. *acuta* Toulmin [closely related to *G. velascoensis* (Cushman)].

The present writers made a study of the planktonic species at Salt Mountain, and found 12 species to occur there (Loeblich & Tappan, 1957). They clearly show a relationship to the Midway group, although representing a younger zone than is found in the Texas section, and younger than the Naheola formation of Alabama, thus agreeing with Toulmin's diagnosis as younger than "Midway."

Planktonic species found in the Salt Mountain limestone and in the lower Paleocene zones are: *Globorotalia angulata, G. perclara, G. elongata, G. pseudomenardii* and *Globigerina triloculinoides.* The following species appear first in the Salt Mountain limestone of Alabama but also are found in the Velasco shale of México, Aquia formation of Virginia and the Hornerstown and Vincentown formations of New Jersey: *Chiloguembelina crinita, Globigerina inaequispira, G. mckannai* and *G. spiralis, Globorotalia acuta, G. apanthesma, G. convexa, G. occlusa* and *G. pseudoscitula.* An unnamed *Chiloguembelina* species occurs in the Salt Mountain and has not been reported elsewhere. The above mentioned species are all representative of the *velascoensis-acuta=spiralis* subzone, *angulata* zone of the upper Paleocene.

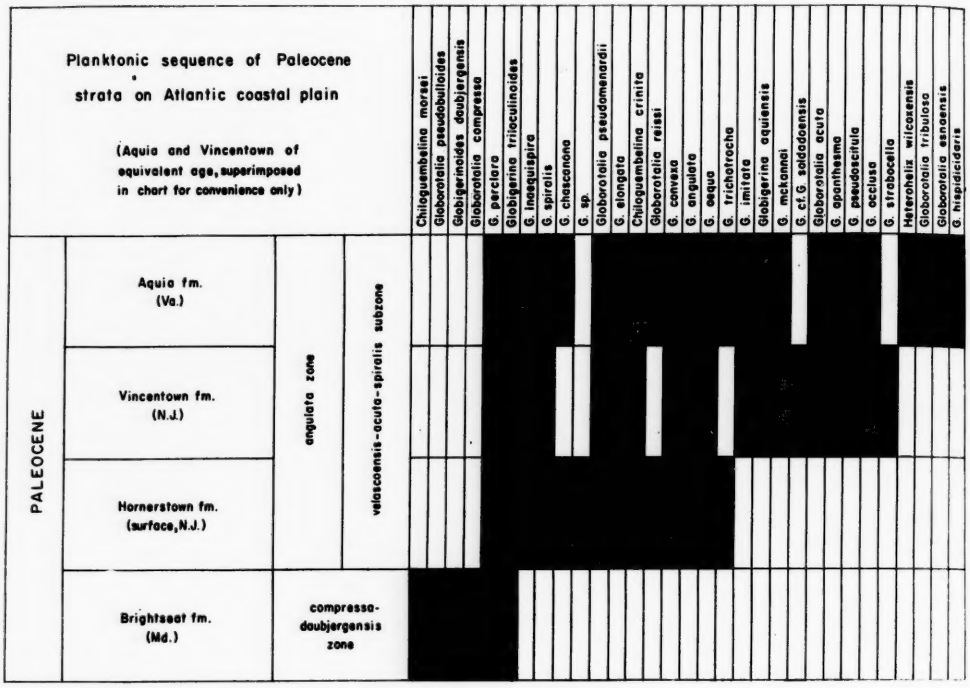
Thus the Salt Mountain has five species in common with lower Paleocene zones in Alabama, including *Globigerina triloculinoides* and *Globorotalia angulata* which do not occur above the Paleocene elsewhere. There are nine species in common with the upper Hornerstown of New Jersey and 14 species in common with the Aquia of Virginia and the Vincentown of New Jersey and 11 found in common with the upper Velasco of México. Six species are found in the Salt Mountain and other late Paleocene formations which range upward into the Nanafalia formation. The planktonic assemblage indicates a late Paleocene age for the Salt Mountain limestone and shows that it is older than Nanafalia rather than above the Nanafalia and below the Tuscahoma sand.

*The Brightseat formation of Maryland and the Aquia formation of Virginia.*—The Brightseat formation of Maryland, which underlies the Aquia formation, was recently described (Bennett & Collins, 1952) and determined to be of Paleocene age on the basis of Foraminifera and megafossils (the latter studied by Julia Gardner). The Brightseat planktonic Foraminifera have been recently described (Loeblich & Tappan, 1957) and represent the *daubjergensis-compressa* faunal zone, of Danian, lower Paleocene, age (Text. fig. 5).

The following species occur in the Brightseat: *Chiloguembelina morsei* (Kline), *Globigerina triloculinoides* Plummer, *Globigerinoides daubjergensis* (Bronnimann), *Globorotalia compressa* (Plummer), *G. pseudobulloides* (Plummer) and *G. perclara* Loeblich & Tappan. All of these are found in equivalent strata of this faunal zone, i.e., type Danian, type Montian, Kincaid and Wills Point formations of Texas, and Pine Barren and McBryde members of the Clayton formation of Alabama.

The Aquia formation of Maryland has been considered by the U. S. Geological Survey to be lower Eocene in age.

Cooke & Stephenson (1928) considered the Aquia and Vincentown equivalent in




TEXT-FIG. 5

age and both to belong to the Wilcox Eocene. Miller (1956) concurred in this determination, on the basis of the megafossils.

Shifflet (1948) described the Foraminifera of the Aquia, stating (p. 17) that it was "considered equivalent to the lower Wilcox of the Gulf Coast and to the Ypresian of Europe," and that the Hornerstown marl and Vincentown sand of New Jersey are equivalent to the Aquia formation. She recorded nine species of planktonic Foraminifera within the fauna. An examination of the type specimens (in the U. S. National Museum) shows these species to be as follows:

*Globigerina compressa* Plummer (recorded only, no specimen deposited in Museum)
*G.* cf. *G. ouachitaensis* Howe & Wallace = *G. spiralis* Bolli
*G.* cf. *G. pseudobulloides* Plummer = *Globorotalia perclara* Loeblich & Tappan
*G. triloculinoides* Plummer = *G. triloculinoides* Plummer
*Globorotalia* cf. *G. angulata* (White) = *G. angulata* (White)
*G. membranacea* (Ehrenberg) = *G. pseudomenardii* Bolli
*G. wilcoxensis* Cushman & Ponton = *G. aequa* Cushman and Renz
*G. wilcoxensis* Cushman & Ponton var. *acuta* Toulmin
*Guembelina wilcoxensis* Cushman & Ponton = *Chiloguembelina crinita* (Glaessner)

The following 24 species of planktonic Foraminifera were described and illustrated from the Aquia formation (Loeblich & Tappan, 1957): *Heterohelix wilcoxensis* (Cushman & Ponton), *Chiloguembelina crinita*, *Globigerina aquiensis* Loeblich & Tappan, *G. spiralis*, *G. inaequispira*, *G. chascanona* Loeblich & Tappan, *G. triloculinoides*, and *G. mckannai*, *Globorotalia tribulosa* Loeblich & Tappan, *G. trichotrocha* Loeblich & Tappan, *G. perclara*, *G. convexa*, *G. hispidicidaris* Loeblich & Tappan, *G. angulata*, *G. reissi*, *G. acuta*, *G. apanthesma*, *G. occlusa*, *G. pseudoscitula*, *G. pseudomenardii*, *G. elongata*, *G. imitata*, *G. aequa* and *G. esnaensis*(?) Le Roy.

Approximately one-half of these species do range upward into the Nanafalia formation (lower Eocene) but the occurrence of the zonal markers *Globorotalia angulata*, *G.*

*acuta* and *Globigerina spiralis*, as well as *G. triloculinoides*, *G. mckannai* and *Globorotalia pseudoscitula*, none of which range into the Eocene, clearly shows that the Aquia must be referred to the *velascoensis-acuta-spiralis* subzone, *angulata* zone of the late Paleocene. This same fauna occurs in the Paleocene of France and England, in Russia, in México and in the Caribbean as well as in the closely related Salt Mountain limestone of Alabama and in the upper part of the Hornerstown and Vincentown formations of New Jersey.

*The Hornerstown and Vincentown formations of New Jersey.*—One of the most controversial formations in this part of the geologic column is the Vincentown formation. Named from Vincentown, in Burlington County, New Jersey, where the deposit was said to be well developed, Clark, Bagg, & Shattuck (1897, p. 326) placed it in the following sequence:

Eocene.....Shark River formation

Upper Cretaceous—
- Manasquan formation
- Rancocas formation..... — Vincentown limesands; Sewell marls
- Monmouth formation..... — Redbank sands; Navesink marls; Mount Laurel sands
- Matawan formation..... — Hazlet sands; Crosswicks clays

The Vincentown was described (p. 338) as consisting of "highly calcareous greensands, the calcareous element being supplied by the vast number of Bryozoan shells which crowd the beds. . . . The Vincentown lime-sands have a constant thickness of about 20 feet in northern and central New Jersey, but increase gradually to the southward and in Salem county suddenly expand until they attain a thickness of about 100 feet." Glauconite is found in all of these deposits. The Sewell, which underlies the Vincentown, was later renamed the Hornerstown marl, as the name Sewell was preoccupied by a formation of Pennsylvanian age.

Clark, Bagg & Shattuck (pp. 357–358) suspected that an unconformity probably existed between the Monmouth and Rancocas formations, and that the Matawan-Monmouth faunas were closely related to one another and sharply defined from the Rancocas-Manasquan-Shark River faunas. The Matawan-Monmouth was considered correlative with the Eutaw-Rotten Limestone-Ripley faunas of the Gulf and the Rancocas-Manasquan-Shark River sequence was considered to represent an interval absent in the Gulf Coastal region, and to represent the time break between the Upper Cretaceous and the Eocene. As compared with the European stages, the Matawan-Monmouth was thought to be probably Senonian, the Rancocas-Manasquan to be Danian and the Shark River, lowest Eocene.

The present classification recognized by the U. S. Geological Survey treats the Vincentown sand as the upper formation of the Rancocas group. (Wilmarth, 1938, p. 2250).

Weller (1907, p. 178) recognized two major paleontologic divisions in the area, the lower he termed "Ripleyian" and the upper "Jerseyian." The line of separation lies between the top of the Tinton sand member of the Redbank sand and the overlying Hornerstown marl. Weller did not consider this faunal change to represent an intersystemic boundary.

Stephenson (Cooke & Stephenson, 1928, p. 141), noted the striking dissimilarities between the "Ripleyian" and "Jerseyian" faunas, and suspected that the latter was perhaps not Cretaceous, but in fact Eocene. Field studies by Cooke and Stephenson resulted in an age determination of Eocene for all the "Jerseyian" formations, based both on macrofossil evidence and on the diastrophic evidence that the Hornerstown marl transgressed southward on successively older Cretaceous beds.

Cooke & Stephenson (1928, p. 147) suggested the correlation of the Vincentown with the Aquia formation of Maryland on the basis of fossil evidence and physical similarity. At this time, no Paleocene deposits were recognized in Maryland, nor on the Atlantic Coast, the oldest Tertiary sediments were considered to be of Wilcox Eocene age. Early correlations of the Vincentown as lower Eocene, in this country, did not necessarily exclude the possibility of a Paleocene age, however, for as late as 1938 (Wilmarth) the U. S. Geological Survey did not officially recognize the Paleocene as a distinct epoch.

Canu & Bassler (1933, p. 3), stated that "The Vincentown Bryozoa certainly show close similarity to those of the Maastrichtian and Danian divisions of Europe, with various genera and some identical species and little relationship to the usual Tertiary faunas of either Europe or America. It is true that various characteristic species of the Vincentown fauna are present in the Aquia formation in Maryland referred to the base of the Eocene and likewise that the Clayton limestone at the base of the Eocene (Midwayan) in the Gulf Coastal States contains similar genera. It is evident that the much-discussed subject of the Cretaceous-Tertiary boundary line is again in question."

Jennings (1936) correlated the Hornerstown and Vincentown formations of New Jersey with the Aquia of Maryland and the lower Wilcox (Nanafalia) of Alabama.

Brotzen (1948, p. 32) in describing the Swedish Paleocene Foraminifera, correlated the Vincentown with the Thanetian and Landenian (he used this latter stage as equivalent to Sparnacian of other authors) and in part with lower Eocene (Ypresian). He also correlated the Kincaid formation (lower Midway group) with Danian, and the Wills Point formation (and the Hornerstown formation of New Jersey) with Seelandian. Above the Midway he considered the lower Wilcox to be of Paleocene and early Eocene age (including Thanetian, Landenian and Ypresian equivalents). His correlations were based in large part on the benthonic Foraminifera, although he mentioned that the Midway "Globigerinidae" occur in the lower Paleocene of Sweden. The upper Paleocene was not then recorded in Sweden, other than as erratic blocks, and the fauna was not known.

McLean (1953, p. 1) noted that both the Hornerstown and Vincentown formations contained benthonic Foraminifera identified by him as of Paleocene age. He further stated that the Vincentown contained other faunal elements suggestive of the Wilcox Eocene, and that "The possibility exists that the Vincentown is a transitional stratal unit."

Fox & Olsson (1955, p. 736) studied the microfauna of various late Cretaceous and early Tertiary formations in New Jersey and concluded that the Hornerstown was probably Paleocene, because 31 species of Foraminifera found therein are restricted to the Midway group on the Gulf Coast. The Vincentown was said to contain "a mixture of typical Paleocene forms in association with new Eocene elements characteristic of the upper part of the Vincentown. It is assumed that the Paleocene forms have been largely reworked into the lower five feet of the Vincentown where they occur with fragments of *Oleneothyris*, *Gryphaea* and *Polorthus* and with considerable reworked typical Hornerstown greensand." They added that "the type Vincentown is clearly Eocene in age."

Hofker (1955, p. 1) also made a study of Vincentown Foraminifera, and concluded that the Vincentown formation is of Paleocene age. He listed 22 species of Foraminifera common to the Vincentown and the Paleocene of Europe, and none found in the Upper Cretaceous. One species was known to occur in the Eocene, and he stated (p. 7) "No species entirely characteristic of the Eocene have been noted from the Vincentown material, whereas the evidence for the Paleocene . . . is quite positive and points to a lower Paleocene age for the Vincentown formation fauna." The majority of species studied by Hofker also were benthonic forms, but he did record three species of *Globigerina* (p. 15), stating, "There are three species of *Globigerina* in the Vincentown formation, and they are figured here as *Globigerina* sp., *Globigerina pseudobulloides*, and *Globigerina triloculinoides*. These identifications (the two given names in the plates) may not be the species referred to, and they may, in fact, all be new species. However, it

is not within the scope of this paper to formally describe or name them, so they are simply figured here for future reference."

The figured and unfigured specimens of *Globigerina* of Hofker's paper were sent for deposit to the U. S. National Museum, mounted on a single slide. On separation, *Globigerina* sp. of Hofker is here referred to *Globigerina mckannai* White and the remainder of his specimens belong to *G. triloculinoides* Plummer and *G. inaequispira* Subbotina. No specimens of *G. pseudobulloides* Plummer were found among Hofker's types, nor do the figures of Hofker (1955, pl. 4) closely resemble that species. The specimen figured as *Globorotalia* (*Truncorotalia*) *lacerti* Cushman & Renz (misspelled *lacerta* on plate 1 of Hofker) is a young specimen of *Globorotalia acuta* Toulmin.

McLean (1955, p. 22) stated that he found "no agreement between published Wilcox Foraminiferal faunas and the Vincentown material, except for the well-known study by Toulmin on the Salt Mountain formation which he regards as of Wilcox age, but which others regard as being Paleocene in age. On the other hand, . . . the Vincentown has many good similarities to Paleocene faunas."

McLean also submitted Vincentown material to other specialists, whose opinions he then quoted. The ostracodes were evaluated by Nadeau (p. 26), who stated that they suggested a lower Eocene age.

Troelsen (*in* McLean, 1955, p. 27) referred the "Vincentown to the Danian-Paleocene transition zone."

Knipscheer (*in* McLean, 1955, p. 28) believed the planktonic Foraminifera from the Vincentown to be "definitely indicative of a Paleocene age for that formation." He added that it was probably upper Paleocene, rather than lower, and that "The frequency of species of *Globorotalia* definitely excludes an Upper Cretaceous age for the sample."

Miller (1956, p. 731) studied the invertebrate fauna of the Vincentown and concluded that the "strongest affinities are to the lower Eocene (Aquia) of Maryland and the Danian of Denmark." He recorded 18 species common to the Vincentown and Aquia, including Bryozoa, ostracods, alcyonarids, and mollusca. However, as the Aquia was considered lower Eocene, he also correlated the Vincentown with the lower Eocene. He stated (p. 732) that the "*Nautilus*" *danicus*, Bryozoa, and alcyonarids were also found in the Danian of Europe, but he considered them "facies fossils."

Loeblich & Tappan (1957) described the planktonic Foraminifera of the Hornerstown and Vincentown formations, recognizing the *daubjergensis-compressa* zone (lower Paleocene, Danian) in the lower Hornerstown of subsurface sections, the *pseudobulloides* subzone, *angulata* zone in middle Hornerstown, subsurface, and the *velascoensis-acuta-spiralis* subzone, *angulata* zone, in the upper Hornerstown of the outcrop and the Vincentown formation.

The Hornerstown formation, at the outcrop, contains the following 14 planktonic species: *Globigerina triloculinoides*, *G. inaequispira*, *G. chascanona*, *G. spiralis*, *G.* sp., *Globorotalia aequa*, *G. trichotrocha*, *G. elongata*, *G. pseudomenardii*, *G. reissi*, *G. perclara*, *G. convexa*, *G. angulata* and *Chiloguembelina crinita*. Only *Globigerina spiralis*, of the upper subzone markers, is found in the Hornerstown and in the lowest Vincentown, just above the contact, on Shingle Run, one mile north of New Egypt, Monmouth County, New Jersey. Possibly an additional subzone could be erected for this part of the section, but more sections are required for study before this would be advisable. The presence of *Globorotalia angulata* and *Globigerina spiralis* and the absence of *Globorotalia pseudobulloides* all indicate an age later than the *pseudobulloides* subzone, and the upper Hornerstown and basal Vincentown are here considered to represent the oldest part of the *velascoensis-acuta-spiralis* subzone.

Fox & Olsson (1955) in studying the benthonic Foraminifera stated that the "Paleocene" species occurring in the Vincentown were reworked into the lower five feet of section. The presence of *Globigerina spiralis* in both the Hornerstown and basal Vincentown formations at the Shingle Run locality, together with the lack of *Globorotalia acuta*, places these strata in the lower part of the upper subzone of the *angulata* zone, both definitely above the *pseudobulloides* subzone. The *velascoensis-acuta-spiralis* subzone, with its complete assemblage, is found in the Vincentown formation at its type lo-

cality, which does not expose the base of the formation. Here a planktonic fauna of 19 species is found: *Globigerina triloculinoides, G. inaequispira, G. mckannai, G. spiralis, G. aquiensis, G.* cf. *G. soldadoensis* Bronnimann, *Chiloguembelina crinita, Globorotalia acuta, G. aequa, G. angulata, G. apanthesma, G. convexa, G. elongata, G. imitata, G. occlusa, G. perclara, G. pseudomenardii, G. pseudoscitula,* and *G. strabocella* Loeblich & Tappan. Only eight of these species range into the lower Eocene and such species as *Globigerina triloculinoides, G. spiralis, G. aquiensis, Globorotalia acuta, G. angulata, G. apanthesma, G. pseudoscitula* and *G. occlusa* definitely indicate a late Paleocene age. The apparent discrepancy in correlation shown by the planktonic Foraminifera with correlations previously based on other groups of organisms is more apparent than real. Many of these varying correlations are made to horizons or stages in other areas, which have already been shown to be partially or wholly equivalent in age.

The Hornerstown and Vincentown were referred to the Upper Cretaceous (Danian) by Clark, Bagg, & Shattuck, the original authors of the name, and by Canu & Bassler to the Maestrichtian and Danian, on the basis of the Bryozoa (although they also considered it similar to the Midway). As shown above, the Danian should be transferred to the Paleocene, and is equivalent in age to the lower Midway. The Hornerstown does include beds of Danian age in the lower part, although the upper Hornerstown and Vincentown are equivalent to the somewhat younger Midway strata of Alabama.

Cooke & Stephenson (1928), Jennings (1936), and Miller (1956) regarded the Vincentown and Aquia as equivalent in age, which is substantiated by the present study. Jennings also considered the Nanafalia formation of Alabama as equivalent (which is here shown to represent the Ypresian or earliest Eocene). The similarity of the Aquia and Vincentown faunas to those of both the Danian and Midway as noted by Canu and Bassler, and by Miller, was not due to "facies fossils," but to the near age equivalence of the enclosing strata, for the type Danian and type Montian are the age equivalents of the Paleocene lower Midway. McLean, Hofker, Knipscheer, Troelsen, and Brotzen all correctly regarded the Vincentown as equivalent to the Paleocene, only Knipscheer correctly determining its upper Paleocene age (although Brotzen considered it to include Thanetian and Landenian equivalents as well as Ypresian). Troelsen was also correct in assigning the Vincentown a post-Danian age.

Even the correlation of the Vincentown formation with the Eocene by Fox & Olsson (1955) may not be greatly at variance with the present paper, for their published abstract did not state whether this correlation referred to the Aquia, the Salt Mountain, lower Wilcox, etc., or to which faunal zone or European stage.

*Wilcox group.*—The Wilcox group is recognized by the U. S. Geological Survey (Wilmarth, 1938, p. 2333) to be of lower Eocene age, and to designate "deposits overlying the Midway and underlying the Claiborne in the Gulf Coastal Plain." Recent studies (Murray, 1955) have shown the "basal Wilcox" of some areas to be the time equivalent of the Midway of other localities. The recognizable sedimentary facies of the Midway and Wilcox groups are thus not exact time units, leading to erroneous conceptions of the time range of various species. Although the Wilcox is considered to be lower Eocene, beds in other areas have been referred to the Wilcox, because of similar lithology, etc., which are faunally much closer to the Midway (Paleocene).

As was demonstrated by Murray (1955), confusion has arisen by the varying usage of the terms Midway and Wilcox by some writers in a lithologic sense (rock unit) and by others in a time connotation (time-rock unit). The greater use of the European stage names or of faunal zones in determining correlations would avoid these misinterpretations.

In the area concerned in the present study the lower Eocene is largely represented by nonmarine sediments. Formations previously referred to the Wilcox that contained planktonic Foraminifera were the Nanafalia and Salt Mountain formations of Alabama. As discussed above, the Salt Mountain fauna shows its equivalency to the Vincentown, Aquia and upper part of the Velasco formations. It contains the latest Paleocene faunal assemblage, and we therefore regard

it as late Paleocene, and better placed as the upper formation of the Midway group of Alabama.

In contrast, the Nanafalia formation has a somewhat different faunal assemblage (see fig. 4). Many of the typical Paleocene species are absent, and others occur that are characteristic elsewhere of lower Eocene. *Globigerina triloculinoides* Plummer, which was present throughout the Paleocene, does not occur in the Nanafalia, nor does *G. mckannai*, *G. spiralis*, *Globorotalia velascoensis*, *G. acuta*, *G. angulata*, *G. occlusa* or *G. pseudoscitula*. In general, the lowest Eocene, or Ypresian stage, in more offshore marine sections, is characterized by a *Globigerina-Globorotalia-Truncorotaloides* assemblage, the last named genus making its first appearance. *Truncorotaloides* (similar to the keeled *Globorotalia* but with supplementary apertures on the spiral side) has not yet been observed in the Nanafalia. However, certain lower Eocene zone species do appear in the Nanafalia, such as *Globorotalia rex* and *G. pseudotopilensis*, allowing a definite correlation of the Nanafalia with the Ypresian and with the lower part of the Upper Lizard Springs formation of Trinidad.

Samples of Wilcox age, Seguin formation, Solomon's Creek member, at the type locality of this member in Bastrop County, Texas, did not contain any planktonic species. However, a planktonic assemblage of the Nanafalia, from various localities in Wilcox and Marengo counties, Alabama, was described by Loeblich & Tappan (1957), and contains 17 species: *Globigerina inaequispira*, *G. chascanona*, *Chiloguembelina crinita*, *Globorotalia aequa*, *G. convexa*, *G. elongata*, *G. esnaensis*, *G. imitata*, *G. irrorata*, *G. perclara*, *G. pseudomenardii*, *G. pseudotopilensis*, *G. reissi*, *G. rex*, *G. strabocella* Loeblich & Tappan, *G. tribulosa* and *G. troelseni* Loeblich & Tappan. *Globorotalia rex* is the zonal marker for the lowest Eocene and *G. pseudotopilensis* is similar to species of the Eocene genus *Truncorotaloides* although not developing the spiral supplementary apertures.

## SUMMARY

*Cretaceous-Paleocene boundary.*—A very pronounced faunal break is shown by the planktonic Foraminifera at the Cretaceous-Tertiary boundary. The genera characteristic of the Cretaceous which do not occur in post Maestrichtian strata include: *Globigerinelloides*, *Planomalina*, *Hastigerinoides*, *Schackoina*, *Praeglobotruncana*, *Rotalipora*, *Globotruncana*, *Rugoglobigerina*, *Abathomphalus*, *Guembelitriella*, *Pseudotextularia*, *Pseudoguembelina*, *Gublerina*, *Planoglobulina* and *Racemiguembelina*. In addition, *Heterohelix*, *Guembelitria* and *Biglobigerinella* are more diversified in the Cretaceous but do range somewhat into the Tertiary. After the extinction of the above genera a new expansion of the planktonic Foraminifera began in the Tertiary. The oldest Tertiary (Danian) is characterized by the genera *Chiloguembelina*, *Woodringina*, *Globigerina*, *Globigerinoides* and nonkeeled *Globorotalia*. Thus the generic assemblage of planktonic forms in the Paleocene is the most restricted since the mid-Cretaceous. The generic assemblage of planktonic Foraminifera in the Danian and its equivalents definitely excludes the possibility of a Cretaceous age.

Whether or not there is physical evidence of an unconformity in most areas now available for study, a considerable lapse of time between the deposition of the latest Cretaceous and earliest Paleocene (Danian) sediments is suggested by the almost complete change in the character of the planktonic faunas. The complete extinction of the Globotruncanidae and most of the Heterohelicidae, and the development of the new Cenozoic assemblage of Globorotaliidae and Orbulinidae was also paralleled by the extinction of the Cretaceous ammonites, rudistids, mososaurs, etc., at the close of the Maestrichtian, emphasizing the relationship of the Danian to the Paleocene, and its separation from the Cretaceous. Furthermore, there is commonly a Maestrichtian-Danian unconformity and the Danian in particular is quite variable in extent and thickness, in accordance with the local structural highs and lows.

*Correlations within the Paleocene.*—The same sequence of planktonic Foraminifera occurs in the Paleocene throughout the world. The lower Paleocene (Danian = Montian) is characterized by a restricted "*Globigerina*" assemblage, here termed the *daubjergensis-compressa* faunal zone. The middle and upper Paleocene (Landenian, or Thane-

tian and Sparnacian) is characterized by an assemblage of keeled *Globorotalia*.

The type Danian and type Montian are shown to be age equivalents of different facies, and should be included as the lower stage of the Paleocene. The type Danian includes strata of both lithologic facies and this term seems preferable for the stage. Strata of Danian age include the Kincaid and Wills Point formations, Midway group of Texas, the Clayton formation, Midway group of Alabama, the Brightseat formation of Maryland, and lower Hornerstown formation of New Jersey.

The Landenian or *angulata* zone is also subdivided into faunal subzones, the lowest or *pseudobulloides* subzone being present in the upper part of the "Danian" at Biarritz, France, the middle part of the lower Lizard Springs formation of Trinidad, the Porters Creek clay and Naheola formation, Midway group of Alabama, and the subsurface Hornerstown formation of New Jersey. The upper Landenian (*velascoensis-acuta-spiralis* subzone) is found in the Russian Caucasus, the Paleocene of Biarritz, the type Thanetian of England, the upper part of the Lower Lizard Springs formation of Trinidad, the upper Velasco formation of Mexico, Salt Mountain formation of Alabama, Aquia formation of Maryland, upper part of the Hornerstown formation and the Vincentown formation of New Jersey.

The planktonic sequence thus solves many of the apparent inconsistencies in correlation of the above mentioned strata.

Scott's early correlation of the Midway and Danian, as well as Gardner's correlation of the Midway as Montian and Landenian, are now seen to have both been correct, for the Midway of the Texas outcrop, where Scott worked, is of Danian (=Montian, lower Paleocene) age, and the upper Midway of Alabama is of Landenian age.

Toulmin was correct in considering the Salt Mountain limestone of Alabama younger than the Midway of Texas, and its close relationship to both the Midway group, as previously defined, and the Wilcox group, is due to its stratigraphic position between these horizons, and not post-Nanafalia as had been supposed. It is late Paleocene in age.

The various correlations of the Vincentown and Hornerstown formations of New Jersey with Danian, Paleocene, and Eocene are understandable also, when its true position is understood, and the Danian correctly regarded as Paleocene rather than Cretaceous. It is seen to be an exact age equivalent of the Salt Mountain and Aquia formations, and also of the "Midway" group, although these opinions as previously stated seemed at variance.

The Vincentown, Velasco and Lizard Springs formations, all of which were in the past referred to the Cretaceous, as was the Danian, are now placed in true stratigraphic position, the Velasco and lower Lizard Springs formations representing the entire Paleocene.

The occurrence of a lower Paleocene zone without angular *Globorotalia* in world-wide extent explains the absence of this assemblage in the type Danian far better than a boreal environment, as similar *Globorotalia* are not so restricted geographically in other regions.

*The Paleocene-Eocene boundary.*—As the upper part of the Paleocene in the type area is nonmarine (the Sparnacian), there is difficulty in correlating with it the marine sections elsewhere and in determining the upper limit of the Paleocene in areas where there was continuous marine deposition. Thus marine beds of equivalent age in one region may be termed Paleocene and in another area are classed as lower Eocene.

There is a distinct generic and specific change in the planktonic fauna of Foraminifera in marine strata at the Paleocene-Eocene boundary. In the lower Eocene (Ypresian) the great Tertiary expansion of planktonic Foraminifera continued with the development of *Truncorotaloides*, followed in the middle Eocene by six additional genera of the Hantkeninidae and Orbulinidae, and an additional three new ones in the upper Eocene.

Nevertheless, there has been some disagreement in the past as to whether the Paleocene-Eocene boundary should be placed at the base or top of the *Globorotalia velascoensis* zone. In México and Trinidad, this zone is placed within the Paleocene, and the type Thanetian, which is generally accepted as Paleocene, and the Paleocene of the Biarritz area of France also include this zone. In

Russia, the *velascoensis* zone is placed in the lower Eocene, and the Aquia, Vincentown and Salt Mountain formations of the eastern and Gulf Coasts of the United States, which contain this faunal zone, although *G. acuta* has replaced the *G. velascoensis*, have each been placed in lower Eocene by some geologists.

The same faunal zonation and sequence is found world-wide, with only the boundary limits of the Paleocene-lower Eocene differently placed.

The evidence of the planktonic Foraminifera places the *velascoensis* zone within the Paleocene, as there is a distinct faunal break at its upper boundary, and only a very minor one at the lower boundary. In the Trinidad section, Bolli (1957) recorded 38 planktonic species in the Lizard Springs formation, and showed that only one species is restricted to the *velascoensis* zone and the overlying lower Eocene, whereas four species of planktonic Foraminifera occur in the *velascoensis* zone and range downward into underlying Paleocene zones also. Seven species first appear just above the *velascoensis* zone and range upward through the lower Eocene, accentuating the faunal break at the upper limit.

In the section here studied there is also a pronounced faunal break at the upper limit of the *velascoensis* zone, indicated by the absence in the Lower Eocene *rex* zone of the many Paleocene species, such as *Globigerina triloculinoides*, *G. mckannai* and *G. spiralis*, *Globorotalia acuta*, *G. angulata*, and *G. apanthesma*, and the appearance of new species such as *Globorotalia rex* and *G. pseudotopilensis*. The *velascoensis* zone is regarded as Paleocene where it is found in Europe, México and Trinidad, hence must also be so regarded in the Gulf and Atlantic Coastal region where it appears in the Salt Mountain limestone, Aquia and Vincentown formations. Furthermore, the presence of the *velascoensis* zone in the type Thanetian of England is conclusive proof of its Paleocene age.

Zonation by the planktonic Foraminifera is thus seen to afford a more accurate means of correlation of marine Tertiary strata than has previously been available for certain of these formations. In nearly every case this evidence is not contradictory to that supplied by other methods of correlation, but substantiates earlier age designations and solves stratigraphic problems for which a solution had not previously been determinable.

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JOURNAL OF PALEONTOLOGY, VOL. 31, NO. 6, P. 1138–1147, 5 TEXT-FIG., NOVEMBER 1957

# LABORATORY STUDIES ON THE RATE OF GROWTH OF THE FORAMINIFER, "*STREBLUS BECCARII* (LINNÉ) VAR. *TEPIDA* (CUSHMAN)"

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ABSTRACT—Many generations of "*Streblus beccarii* (Linné) var. *tepida* (Cushman)" have been cultured successfully in the laboratory over a period of two years. During this time, experiments have been carried out on the effects of temperature and salinity upon the rate of growth and reproductive activity.

Temperatures below 10°C. and above 30–35°C. result in a cessation of growth, temperatures lower than 10°C. allow life, but temperatures above the upper extreme cause death in a short time. Between these limits growth is observed, the rate increasing with the temperature. Reproduction takes place at temperatures between approximately 20°C. to 30°C.

Temperature also affects the duration of each generation; at 20°C. it may take four times as long to reach reproductive maturity as at temperatures of 25° to 30°C. Under the latter conditions reproduction occurs on the average of once per month.

Salinities between 20 and 40 °/₀₀ allow normal growth and reproduction. Above and below these limits growth and reproductive activity decline until growth finally ceases at salinities higher than 67 °/₀₀ or below 7 °/₀₀. Reproduction occurs only at salinities between 13 °/₀₀ and 40 °/₀₀. The time required to reach reproductive maturity also increases as the extreme tolerance limits are approached so that it requires twice as long for each generation at 13 °/₀₀ as it does within the normal range.

## INTRODUCTION

FEW experimental data have been published emphasizing the effect of environmental factors upon the Foraminifera. External factors such as temperature and salinity presumably exert a selective effect by direct action on fundamental metabolic processes and undoubtedly play an important role in determining which species will be excluded and which will be found in any given area.

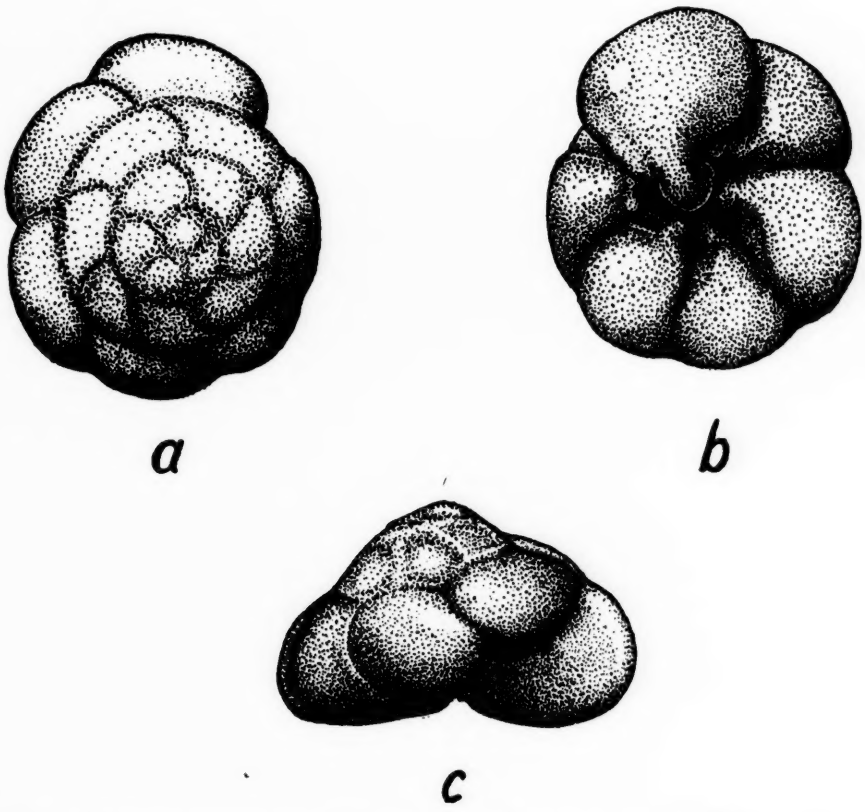
Each species appears to have its own range of environmental conditions within which it will flourish, the limits being determined by its physiological makeup. If a species is continuously exposed to conditions outside these limits it will sooner or later fail in competition with other better-adapted forms and must eventually die out. According to Andrewartha & Birch (1954, p. 26) even slight changes in environmental conditions are shown to affect longevity, fecundity, and rate of development, and these in turn will determine the rate of increase or decrease of the population. Knowledge of these limits and of the reactions of Foraminifera to the extreme conditions of their environment is, therefore, of great importance.

A paper describing the results of some preliminary laboratory experiments on two species of Foraminifera has been published (Bradshaw, 1955). Many of the methods and techniques used for the present study are similar to those used in the earlier work.

The study has been supervised by Fred B. Phleger. The laboratory work was supported in part by a contract of the University of California with the Office of Naval Research, and in part by American Petroleum Institute Project 51. Species illustrations were prepared by Robert R. Lankford. Appreciation is expressed to Dr. Zach M. Arnold of the University of California at Berkeley and Miss Frances L. Parker of Scripps Institution for helpful suggestions received during preparation of this manuscript. This is a contribution from the Scripps Institution of Oceanography, New Series, No. 925. Contribution No. 26, Marine Foraminifera Laboratory.

## MATERIALS AND METHODS

The living specimens of "*Streblus beccarii* (Linné) var. *tepida* (Cushman)" (Text-fig. 1) used in the experiments came from several samples of sediment collected by R. R. Lankford from a depth of six feet in Lower




TEXT-FIG. *1*—"*Streblus beccarii* var. *tepida* (Cushman)," 5×170. a, Dorsal view; b, ventral view; and c, side view.

San Antonio Bay, Texas. The taxonomic status of this variety is in doubt but the name used should sufficiently identify the form. A description has been given by Parker, et al., (1953, p. 13, pl. 4, fig. 25–28).

The following discussion is based largely on test morphology. Laboratory generations appear to follow one another at approximately equal intervals, the exact time depending upon environmental conditions. No good evidence has been seen of a dimorphic alternation of generations and most of the forms, with very few exceptions, have a prolocular diameter of approximately 57$\mu$. According to observations made by Lister (1895, p. 436) on a related form, this size should be indicative of the megalospheric generation. Very rarely, young individuals were observed with a proloculus of approximately 33$\mu$ but these never developed beyond the two-chambered stage and eventually died. Nuclear staining with acetocarmine has, thus far, shown only one nucleus.

The direction of coiling appears to be so distributed that approximately half of the adult specimens coil to the right and the other half turn to the left. The offspring of either a right or left coiled parent have approximately a 50-50 ratio of coiling direction. Changes in temperature or salinity appear to have little effect upon this character. The number of young produced varies from about 17 to 44 individuals, usually averaging from 28 to 32.

The young foraminifer emerges from the parental test at the two-chambered stage (maximum diameter approximately 78$\mu$). At first the young adhere closely to the empty adult but after several hours grad-

ually move away. When food is plentiful and environmental conditions are optimal the addition of chambers is so rapid that three chambers are present by the second day and four chambers by the fourth day. The rate of addition becomes slower as the individual grows larger. Under optimum conditions reproduction occurs at any time after a total of 13 or more chambers has been attained. Reproduction typically terminates the life of the parent, although occasionally some protoplasm showing pseudopodial activity may remain behind in the test for several days before decomposing.

A series of experiments was designed to assess the importance of two environmental factors, temperature and salinity. If hereditary differences can be disregarded it may be assumed that the rate of growth of an individual is directly related to the fitness of its environment. Since it could not be shown that all the individuals had a uniform heredity, an attempt was made to minimize the possible effect of any hereditary differences by selecting the groups of six to ten young Foraminifera in a random manner from the same mass culture.

Watch glasses, containing the young forms were placed in covered petri dishes and kept under the following temperatures at a constant salinity of 33.5°/₀₀. Duplicate cultures were kept at temperatures of 15°, 20° and 30°C.

Rate of growth could be determined either by number of chambers added or linear addition to the maximum test diameter. In the present study chamber number was used. For some purposes, however, linear measurement may be more applicable since this would enable an approximate calculation of protoplasmic volume increase. Text-figure 2 compares the maximum diameter of the test with that of chamber number so that the number of chambers given in the subsequent figures can be converted to linear measurement if desired.

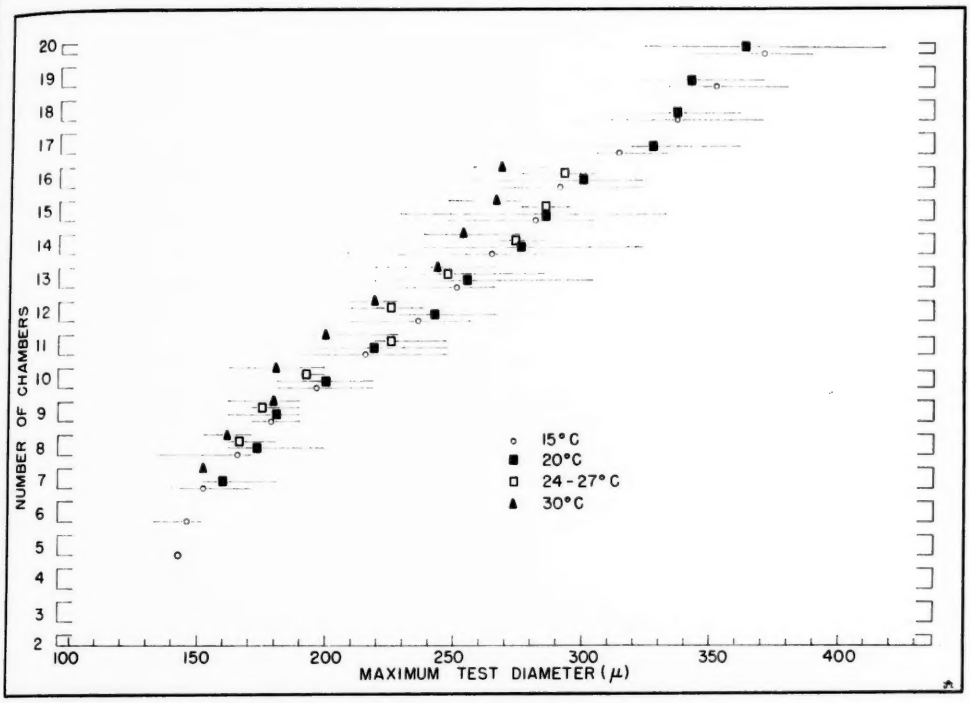
On Monday and Thursday mornings during the course of the experiment the maximum diameter of each individual, at a magnification of 75×, was measured with an ocular reticle and the total number of chambers was counted. Each specimen was then carefully pipetted into a freshly prepared sterile sea water medium and again placed under the prescribed environmental conditions. An "artificial detritus" composed of freshly heat-killed *Chlamydomonas* was used for feeding. Preliminary experiments showed that the addition of approximately 200,000 cells to each culture at equal intervals twice a week was sufficient to allow ten Foraminifera to grow normally.

The curves (Text-fig. 3,4, and 5) showing the rate of growth under various environmental conditions cover the period from the beginning of the experiment to the onset of reproduction. The length of life from birth can be approximated by extrapolation of

| | Temperature °C. | | | | | |
|---|---|---|---|---|---|---|
| | 10° | 15° | 20° | 24–27° | 30° | 35° |
| Mean number of chambers at start of experiment | 10.3 | 7.3 | 8.3 | 8.7 | 8.5 | 8.7 |
| Range of chamber number | 8–17 | 6–9 | 7–11 | 8–11 | 8–9 | 6–11 |
| Number of specimens | 7 | 17 | 16 | 7 | 15 | 9 |

Similar groups (at 24–27°C.) were kept at the following salinities.

| | Salinity °/₀₀ | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 2 | 7 | 13 | 20 | 27 | 30 | 33.5 | 40 | 50 | 67 |
| Mean number of chambers at start of experiment | 9.1 | 8.8 | 9.0 | 8.9 | 9.2 | 8.5 | 8.7 | 7.8 | 8.4 | 9.7 |
| Range of chamber number | 7–11 | 7–11 | 8–10 | 7–12 | 7–10 | 6–10 | 8–11 | 6–10 | 6–11 | 8–11 |
| Number of specimens | 10 | 10 | 8 | 9 | 8 | 10 | 7 | 10 | 10 | 7 |




TEXT-FIG. 2—Relation between chamber number and maximum test diameter. Symbols indicate the mean maximum test diameter and the observed range of the specimens cultured at different temperatures.

these observed growth curves. The length of time from birth to reproductive maturity will vary somewhat among the different individuals of a culture. For the purposes of graphic representation the first occurrence of reproduction in each culture marks the end of that particular experiment. In the text discussion, however, the average length of life of all the specimens in each culture has been used when comparing the results of environmental influences.

## EXPERIMENTAL RESULTS

### *Temperature Experiments*

Text-figure 3 shows the mean rate of addition of chambers in cultures containing from six to ten specimens when kept at the indicated temperatures and at a salinity of 33.5‰. At 10°C. no growth was observed. At 15°C. there was some growth amounting to approximately one new chamber every six days. Temperatures of 20°C. permitted one new chamber every four days. At temperatures of 24–27°C. and 30°C., however, the test growth rate was doubled so that one new chamber was added every two days. When cultures were kept at 35°C. no growth was observed and the specimens died within twenty-four hours.

Although no observable growth occurred in cultures kept at 10°C., metabolism did not cease entirely and the individuals appeared to live indefinitely long periods without reproducing. The culture was transferred to room temperatures of 24–27°C. after 27 days of no growth, and the specimens grew rapidly and reproduced 25 days later.

The 15°C. culture grew very slowly for 134 days with no evidence of reproduction; however, at the end of this period, reproduction occurred within eight days when the culture was transferred to temperatures of 24–27°C.

At 20°C. there was one peculiar instance of possible reproductive activity after 72

days. At this time many spherical prolocula or small *Allogronia*-like forms were found embedded in the umbilicus of a mature adult. Normal calcareous tests never developed and the individuals degenerated after several weeks of no growth. This phenomenon has been observed on several occasions and may represent an abortive attempt at reproduction. Seventy-six days after the start of the experiment one specimen had a normal brood but the remaining specimens did not reproduce until 22 days later.

At 24–27°C. the average time from the beginning of the experiment to reproductive maturity was 19 days whereas at 30°C. the main period was only 15 days. At 35°C. the specimens lived less than one day.

The relationship between chamber number and mean maximum test dimension at different temperatures, shown in Text-figure 2 reveals that Foraminifera grown at warm temperatures (30°C.) tend to add chambers having a smaller size than do specimens kept at cooler temperatures. Warm temperatures also seem to encourage the development of misshapen individuals which have chambers of variable size.

There may be a significant difference in the total number of chambers and the maximum test diameter for the parent test at the time of reproduction for specimens cultured at different temperatures, as shown by the following table:

| | Temperature °C | | | |
|---|---|---|---|---|
| | 15°C.* | 20°C. | 24–27°C. | 30°C. |
| Mean number of chambers at reproduction | 20 | 19 | 15 | 15 |
| Range of chamber number at reproduction | 18–21 | 17–21 | 13–17 | 13–17 |
| Mean size at reproduction ($\mu$) | 355 | 357 | 293 | 266 |
| Number of specimens examined | 14 | 9 | 5 | 12 |

* No reproduction at indicated temperature.

*Salinity Experiments*

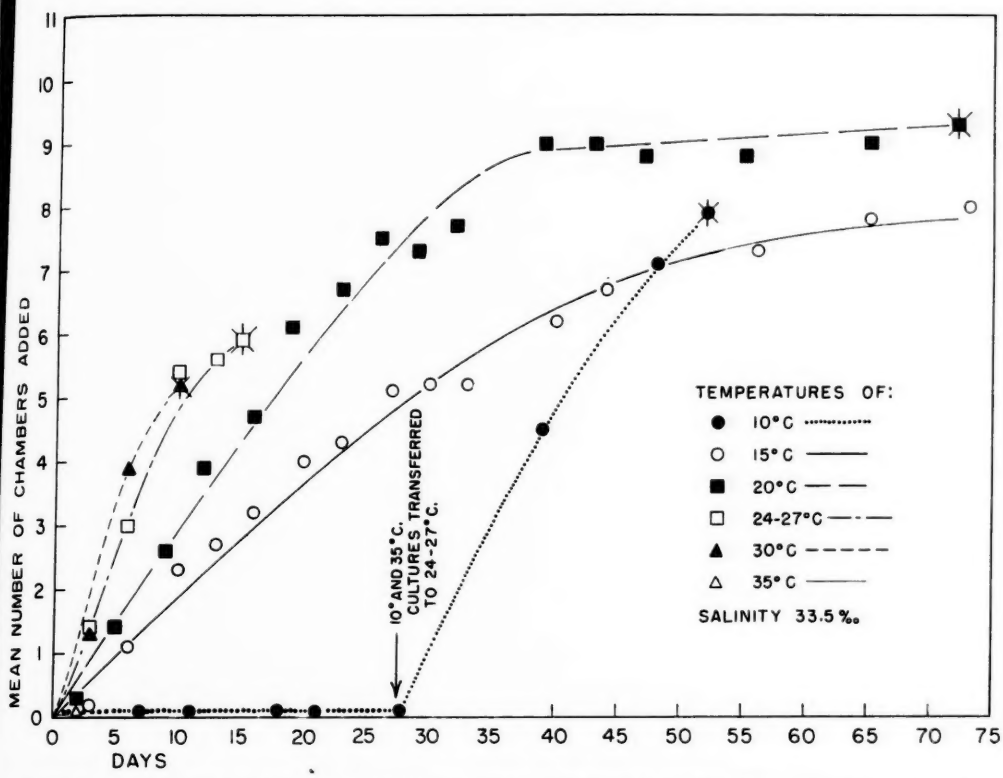
Text-figures 4 and 5 show the mean rate of growth of cultures containing from six to ten specimens when kept at the indicated salinities and at temperatures varying between 24 to 27°C. At salinities of 20–40°/$_{oo}$, one new chamber was added approximately every two days. At salinities of 13°/$_{oo}$ and 50°/$_{oo}$ chambers were added at the rate of one every three days. The culture kept at a salinity of 67°/$_{oo}$ showed no growth for a 35-day period, but was still viable as shown by the resumption of its normal rate of growth when transferred to a salinity of 33.5°/$_{oo}$.

Within the salinity range of 20°/$_{oo}$ to 40°/$_{oo}$, the average length of time for reproduction to occur was 23 days. Specimens kept at 13°/$_{oo}$ required an average of 48 days to reproduce. Below 13°/$_{oo}$ cultures failed to grow, although this may have been partly an effect of low pH as well as salinity.

The tests of specimens grown at 2°/$_{oo}$ and 7°/$_{oo}$ dissolved within a few days after introduction to the experimental media. The pH values were 7.2 and 7.4 respectively, which are too low to allow the existence of carbonate tests. This low pH was a result of the use of distilled water instead of river water in the dilution of the sea water for the experimental media. Natural river water usually contains large amounts of carbonate and other anions which act as buffers to resist the lowering of pH caused by respiration and atmospheric $CO_2$. Distilled water, on the other hand, contains none of these buffers and consequently when it is used to dilute sea water to very low salinity the remaining ions are insufficient to buffer effectively. The experimental results shown for the low salinity cultures, therefore, must not be considered indicative of those to be expected in natural environments where river water is mixed with sea water.

Subsequent experiments using Mississippi River water for dilution have shown slight growth in a salinity of 7°/$_{oo}$ but none in 2°/$_{oo}$ although the Foraminifera remain alive and have intact tests.

Salinities of 50°/$_{oo}$ and higher not only retard growth but also appear to inhibit the reproductive process, since no reproduction occurred during the time the cultures were kept under the experimental conditions.




TEXT-FIG. *3*—Growth of "*Streblus beccarii* var. *tepida* (Cushman)" at different temperatures. * Indicates first occurrence of reproduction in culture.

When transferred to salinities of 33.5°/₀₀, however, the specimens eventually reproduced.

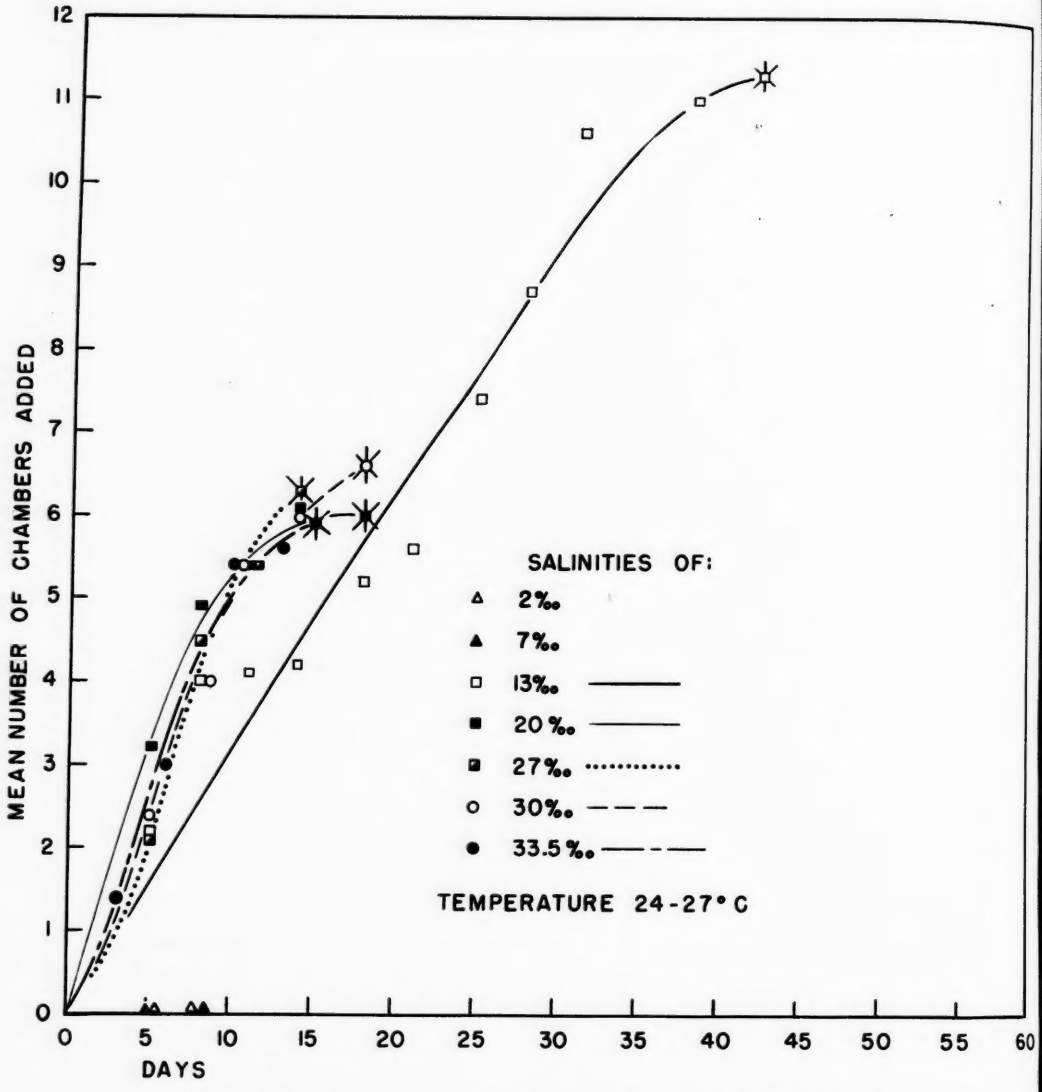
Specimens cultured at different salinities may show a significant difference in the total number of chambers and in the mean maximum test diameter at the time of reproduction. The relationship is shown by the following table:

## DISCUSSION

Experimental results have shown that in the life cycle of "*Streblus beccarii* var. *tepida*," growth and eventually reproduction will take place as long as environmental factors are favorable. Furthermore, as the environmental factors, e.g. temperature and salinity depart from the optimal values, the rate of growth and the frequency of repro-

| | Salinity °/₀₀ | | | | | | |
|---|---|---|---|---|---|---|---|
| | 13 | 20 | 27 | 30 | 33.5 | 40 | 50* |
| Mean number of chambers at reproduction | 19.7 | 18.2 | 17.1 | 16.5 | 15.0 | 18.5 | 18.5 |
| Range of chamber numbers | 17–21 | 17–19 | 15–19 | 15–17 | 13–17 | 16–21 | 15–21 |
| Mean maximum diameter (μ) | 296 | 298 | 293 | 285 | 293 | 300 | 300 |
| Number of specimens | 8 | 9 | 6 | 6 | 5 | 6 | 7 |

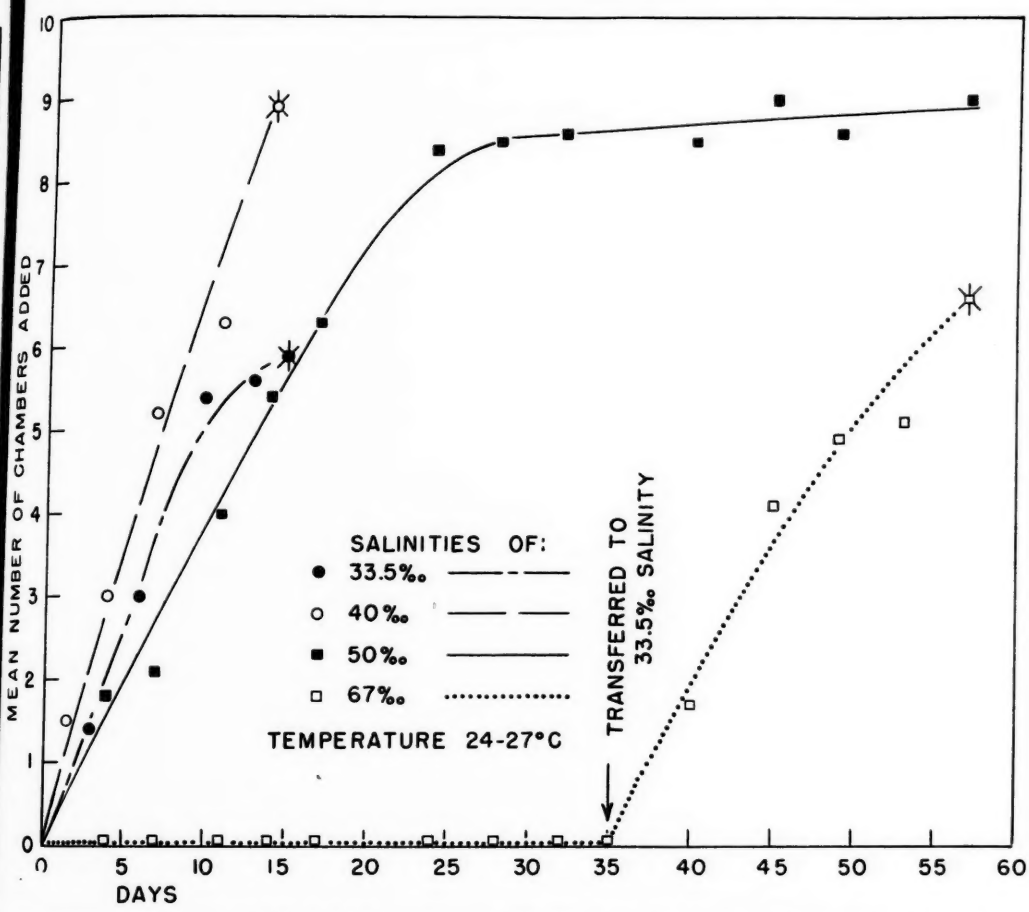
* No reproduction at indicated salinity.




TEXT-FIG. 4—Growth of "*Streblus beccarii* var. *tepida* (Cushman)" at salinities less than that of normal sea-water. * Indicates first occurrence of reproduction in culture.

duction decline. At any given temperature or salinity within the tolerance of the species the growth as measured by rate of chamber increase is not uniform but occurs more rapidly in young individuals and slows down as reproductive maturity is reached. The reason for the decline of growth and subsequent reproduction at the end of life is not known. Mazia (1956) shows that it may not be merely the attainment of a critical size but also the completion of important nuclear processes that "triggers" reproduction in *Amoeba proteus*. This may be true also in the Foraminifera but further studies are necessary.

The present experiments tend to substantiate Mazia's findings. In the experimental cultures of Foraminifera, reproduction has not occurred until a total of at least 13 chambers has been reached. As was true




TEXT-FIG. 5—Growth of "*Strebulus beccarii* var. *tepida* (Cushman)" at salinities greater than that of normal sea-water. * Indicates first occurrence of reproduction in culture.

of *Amoeba*, however, the mere attainment of this size will not in itself guarantee successful reproduction since presumably a period of nuclear reorganization also must precede the production of young forms.

For reproduction to occur the environmental factors must be within certain limits. In the cultures grown under optimum conditions, for example, temperatures of 24–30°C. and 33.5°/₀₀ salinity (Text-figure 3) reproduction occurred soon after the "critical size" was reached.

The cultures kept at 15° and 20°C. and also those at 50°/₀₀ salinity. Text-figures 3 and 5, however, illustrate the situation when conditions are such that reproductive activity cannot easily be carried out. Here, even though the "critical size" has been reached, the reproductive process appears to be inhibited by the prevailing conditions. If the cultures are returned to optimal conditions, however, reproduction usually follows within a few days.

When reproduction is delayed by unfavorable temperatures and salinities, and other factors, food, etc., remain favorable, growth may continue, as long as the conditions are not excessively detrimental. The specimens may thus finally reproduce at a larger size and with a greater number of chambers than would be true under more favorable circumstances.

If the conclusions derived from the laboratory experiments are valid and may be

applied to natural populations of Foraminifera the larger specimens of the same species would be expected in the unfavorable environments and the smaller specimens under the most favorable conditions. Nicol (1944) shows such a relationship between size, temperature and latitude in his study of West Coast species of *Elphidium*. He noted that "increase in size of specimens is related to decrease in temperature and increase in degrees north latitude." He further states that temperature may be the controlling factor although he does not say in what manner the temperature may control the size. Hesse, Allee & Schmidt (1951) state that "the larger size of northern and cold water marine forms is a frequent phenomenon, both as applying to the individuals of a wide ranging species and to the northern or cold water species that replace tropical forms within a given genus. Delayed sexual maturity, which favors growth in size, appears to be directly dependent on retardation of growth at lower temperatures. . . ."

The results from laboratory culture experiments are interesting for they may give us a clue to the behavior of Foraminifera in nature. So long as temperature and other factors remain within a "favorable range" in the laboratory, "*S. beccarii* var. *tepida*" will reproduce continuously with the result that under optimum conditions of 30°C. one generation will follow another at approximately 28-day intervals. Temperatures this high occurring under natural conditions during the summer may allow several generations of this form with the resulting addition of many empty tests to the sediments. Assuming that about 28 young are produced per parent and that all the offspring grow to maturity and reproduce, at the end of three such generations, a total of 22,765 empty tests would have been contributed to the sediments from one ancestral test. This extreme rate of test deposition is not realized in nature because of predation and other factors; nevertheless, there may be a more significant addition of tests to the sediments in the warmer months than during the remainder of the year.

With the advent of more adverse temperatures (20 to 24°C.) in the fall, the growth rate declines and a longer interval is required between successive generations. Reproduction does not occur below approximately 20°C. With temperatures of 10° and lower, such as may occur in the San Antonio Bay area in winter, there should be a complete cessation of growth, although these Foraminifera may remain alive and resume growth when favorable temperatures again occur. In winter the minimal addition of empty tests to the sediments is expected. Myers (1942) has shown similar seasonal changes in growth rate for natural populations (Plymouth, England) of *Elpidium crispum* (Linné). Growth was rapid in spring and summer, declined in the fall and did not occur during the winter.

In "*S. beccarii* var. *tepida*" normal growth and reproduction occur between salinity values of 20°/₀₀–40°/₀₀. Beyond these limits growth and reproductive activity decline until finally growth ceases at salinities higher than approximately 67°/₀₀ or below 7°/₀₀; other life activities may continue, however, at salinities as low as 2°/₀₀ (and perhaps even lower).

A knowledge of the reactions of laboratory cultures of Foraminifera to different salinities makes it possible to explain certain anomalous occurrences under natural conditions. Lankford (personal communication) reported that living specimens of "*S. beccarii* var. *tepida*" were found in water of 1°/₀₀ salinity off the mouth of the Mississippi River. The salinity near the mouths of estuaries may vary widely because of variations in the amount of river discharge, reaching minimal values in winter and spring with maximal values in summer and fall. A station located hear the mouth of the Mississippi River, for example, having a bottom salinity of less than 1°/₀₀ in February was found to have a salinity of almost 32°/₀₀ in November. A form such as "*Streblus beccarii* var. *tepida*," with a high degree of salinity tolerance could be expected to survive these conditions of extremely low salinity and to flourish when conditions are once again within the reproductive range.

It must not be assumed that the results from the preceding experiments will be applicable to all species of Foraminifera. The limited work that has been done so far on the tolerance of Foraminifera shows that many and perhaps most species have narrower limits than these reported for survival

and reproductive activity. It may be possible, however, that in variable environments similar to San Antonio Bay, the results described for "*S. beccarii* var. *tepida*" may serve as a general pattern for other species found in similar habitats.

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JOURNAL OF PALEONTOLOGY, VOL. 31, NO. 6, P. 1148-1153, PL. 143-144, 3 TEXT-FIG., NOVEMBER 1957

# LOWER MISSISSIPPIAN CEPHALOPODS FROM THE ROCKFORD LIMESTONE OF NORTHERN INDIANA

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University of Notre Dame

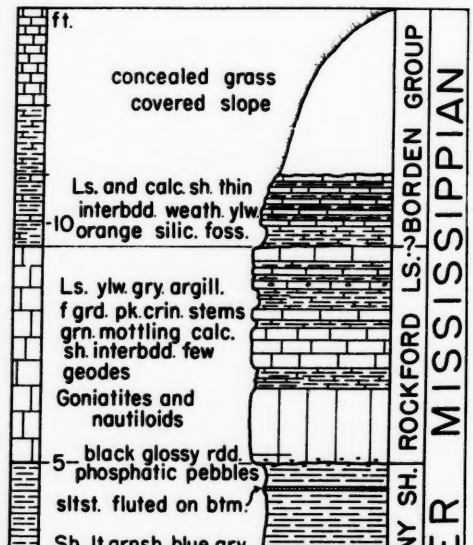
ABSTRACT—A cephalopod fauna represented by sixteen specimens (five goniatites and eleven nautiloids) from the Lower Mississippian (Kinderhookian) Rockford limestone formation obtained from a single locality in northwestern Indiana is described. The goniatites *Gattendorfia alteri*, n. sp., and *Prodromites gorbyi* with supporting evidence from the nautiloids establishes the correlation of these beds with the Rockford of southern Indiana.

## INTRODUCTION

RECENTLY we were able to obtain this important collection of cephalopods from a Lower Mississippian locality in northwestern Indiana. The specimens were collected during several years of quarry operations by Mr. Chris E. Alter who kindly lent them for study. It is significant that these fossils substantiate correlation of the rocks containing them with the Rockford limestone of southern Indiana. The evidence supports Shrock & Malott's (1929, p. 223) assignment of these beds to the Rockford limestone. These authors indicate the presence of goniatite (?) and orthoceratite cephalopods in these beds but give no paleontological details. This small quarry, first described by Collett (1883, p. 69), has long been abandoned and as in the case of the Rockford type locality (Campbell, 1946, p. 856), it is unlikely that additional material will be found from the present exposure; thus this fauna, as far as we know, represents the total number of specimens to come from this location and be preserved. The abandoned quarry is located in Mr. Alter's farmyard along the head of Meadel Ditch (county highway map) near the center of the NW¼ of Section 21, T. 27 N., R. 7 W., Jasper County, Indiana, which is about 3½ miles WNW. of Remington. This paper firmly establishes the presence of Rockford limestone in northern Indiana and presents a supplement to the classic Rockford goniatite limestone fauna of southern Indiana.

The fauna, consisting of eleven nautiloid and five goniatite specimens came, according to Mr. Alter, from the shale partings between the limestone beds in the section formerly quarried. Shrock & Malott measured the section when the quarry was in operation and state that the beds being quarried correspond to the Rockford limestone (Text-fig. 1). They also indicate that the cephalopods came from this interval. The lithology of the limestone matrix adhering to the fossils including the shell fillings is characteristic of these beds.

Cumings (1922, p. 486) summarizes the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concealed grass covered slope
Ls. and calc. sh. thin interbdd. weath. ylw. orange silic. foss.
10
Ls. ylw. gry. argill. f grd. pk. crin. stems grn. mottling calc. sh. interbdd. few geodes
Goniatites and nautiloids
5
black glossy rdd. phosphatic pebbles
sltst. fluted on btm.
Sh. lt. grnsh. blue gry. soft clay, conodonts
after Shrock & Malott 1929, p. 223
NEW ALBANY SH.
ROCKFORD LS.
BORDEN GROUP
LOWER MISSISSIPPIAN

TEXT-FIG. 1—Generalized geologic section measured from outcrop in Alter's farmyard representing section of abandoned quarry.

status of the Kinderhookian Rockford limestone. Subsequent closely related cephalopod studies which have a bearing on the regional relations of the Rockford limestone include Miller & Furnish (Chouteau of Missouri) and Miller & Collinson for Missouri; Miller & Garner for Michigan and Ohio; Miller & Youngquist for New Mexico (Cavallero); Miller, Downs, & Youngquist for Arizona (Redwall); and Hyde (1953), p. 336) for Ohio. Miller & Sweet (Miller & Garner, 1955, p. 157) are re-studying the Ohio Lower Mississippian cepahlopods. Campbell (1956, p. 1679) is continuing his work on the Kinderhook section of southern Indiana which involves clarification of the type Rockford. The stratigraphic relationships taken from the Mississippian Correlation Chart (Geol. Soc. Amer., 1948, chart no. 5) is summarized in Text-figure 2.

The shale beds beneath the Rockford limestone are referred to the New Albany shale (unrestricted) realizing that Campbell (1956, p. 1679) has restricted the New Albany shale to pre-Sanderson Blackiston and Blocher shale units which he considers entirely Devonian. He reports that the type Rockford overlaps unconformably older beds. The contact between the Rockford and underlying shale in the Alter's section is sharp and slightly irregular. The upper inch of shale is weathered to limonitic clay which contains black water-rounded phosphatic pebbles, conodonts, and fossil bone fragments clearly indicating the presence of an unconformity. In addition the shales beneath the Rockford limestone are not the black, fissile type but are more like the Underwood shales of southern Indiana.

The following is a faunal list of the cephalopods obtained from the Rockford limestone of Indiana with citations of the latest pertinent references (modified after Moore, 1928, p. 104):

*Goniatites*

| | |
|---|---|
| **Gattendorfia alteri* n. sp. G. & T. | |
| *Imitoceras rotatorium* (de Koninck) | 1955, Miller & Garner, p. 133 |
| *Münsteroceras oweni* (Hall) | 1955, Miller & Garner, p. 138 |
| *Münsteroceras parallelum* (Hall) | 1951, Miller & Collinson, p. 471 |
| **Prodromites gorbyi* (Miller) | 1951, Miller & Collinson, p. 482 |
| *Protocanites lyoni* (M. & W.) | 1951, Miller & Collinson, p. 479 |

*Nautiloids*

| | |
|---|---|
| **Aipoceras* ? sp. | |
| *Dawsonoceras heterocinctum* (Winchell) | |
| *Dawsonoceras whitei* (Winchell) | |
| *Gyroceras gracile* Hall | 1866, M. & W., p. 164; 1953b, Miller & Garner, p. 128 |
| *Mooreoceras icarum* (Hall) | |
| *Mooreoceras indianense* (Hall) | 1939, Miller & Furnish, p. 165 |
| **Mooreoceras* ? spp. | |
| *Oncodoceras rockfordense* (M. & W.) | |
| **Poterioceras* ? spp. | |
| **Rineceras digonum* (M. & W.) | 1953b, Miller & Garner, p. 114, 123 |
| *Stroboceras trisulcatum* (M. & W.) | 1953b, Miller & Garner, p. 137 |
| **Welleroceras liratum* Miller & Furnish | |

* Alter's quarry.

## SYSTEMATIC PALEONTOLOGY

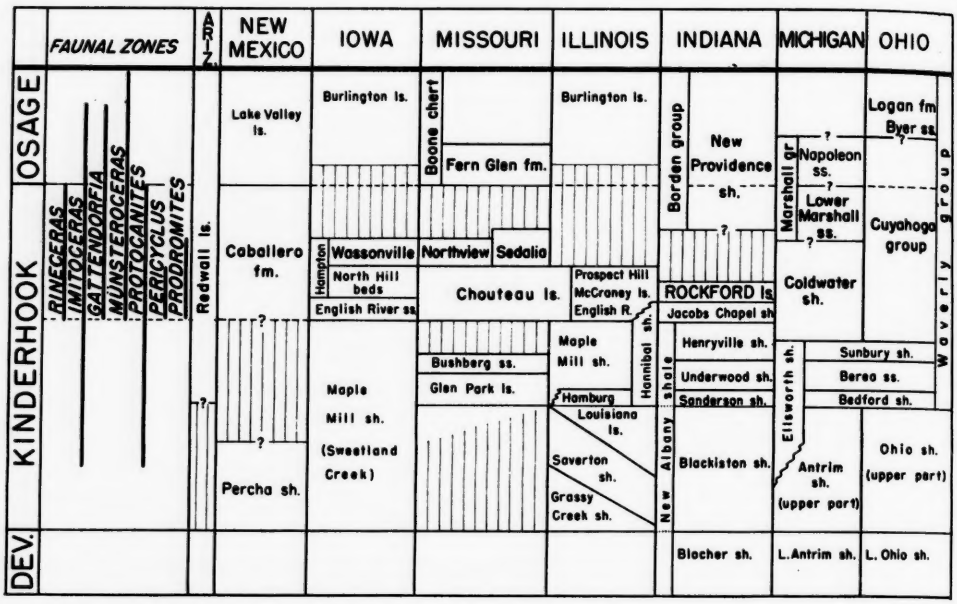
*Subclass Nautiloidea*

*Welleroceras liratum* Miller & Furnish, 1939

Plate 143, fig. 1

This form was originally described by Miller & Furnish (1939, p. 177) from the Chouteau limestone of Missouri. Miller & Youngquist (1947, p. 114) have recognized this species in the Caballero formation of New Mexico.

The Rockford specimen is a large, incomplete, septate, internal mold only moderately well preserved. The length of the phragmocone is about 180 mm.; however, the living chamber and a few early chambers are missing. The nature and position of the siphuncle cannot be determined nor is there any evidence of lirae.




TEXT-FIG. *2*—Stratigraphic chart of selected Lower Mississippian sections showing status of Rockford limestone (Geol. Soc. Amer. Mississippian Correlation Chart with slight modification). Bold lettering indicates formations from which important cephalopods, particularly goniatites, have been obtained.

*Aipoceras* ? sp.
Plate 143, fig. 2

This single, large, incomplete gyroceracone is only moderately well preserved in limestone. The conch resembles *Aipoceras oweni* Miller & Furnish and *Oncodoceras blairi* (Miller) from the Chouteau of Missouri. A comparison between the two on the basis of the following characteristics favored the former genus: general curvature of dorsal and ventral margin, rapidly expanding orad, length and shape of camerae, and shape of cross-section. There is not enough of the living chamber in the Rockford specimen to tell whether or not it is constricted.

The siphuncular position is well defined on the septal wall of the third chamber (Pl. 143, fig. 2) being about half-way between the center and the ventral margin. The septal neck is strongly curved extending at least 4 mm. apicad with a minimum diameter of about 3.5 mm.

*Rineceras digonum* ? (Meek & Worthen)
Plate 143, fig. 6–8

This single, poorly preserved specimen has the general curvature and suture trace resembling *R. digonum magnum* (Miller & Furnish) from the Chouteau of Missouri. The type of this species is from the Rockford of southern Indiana.

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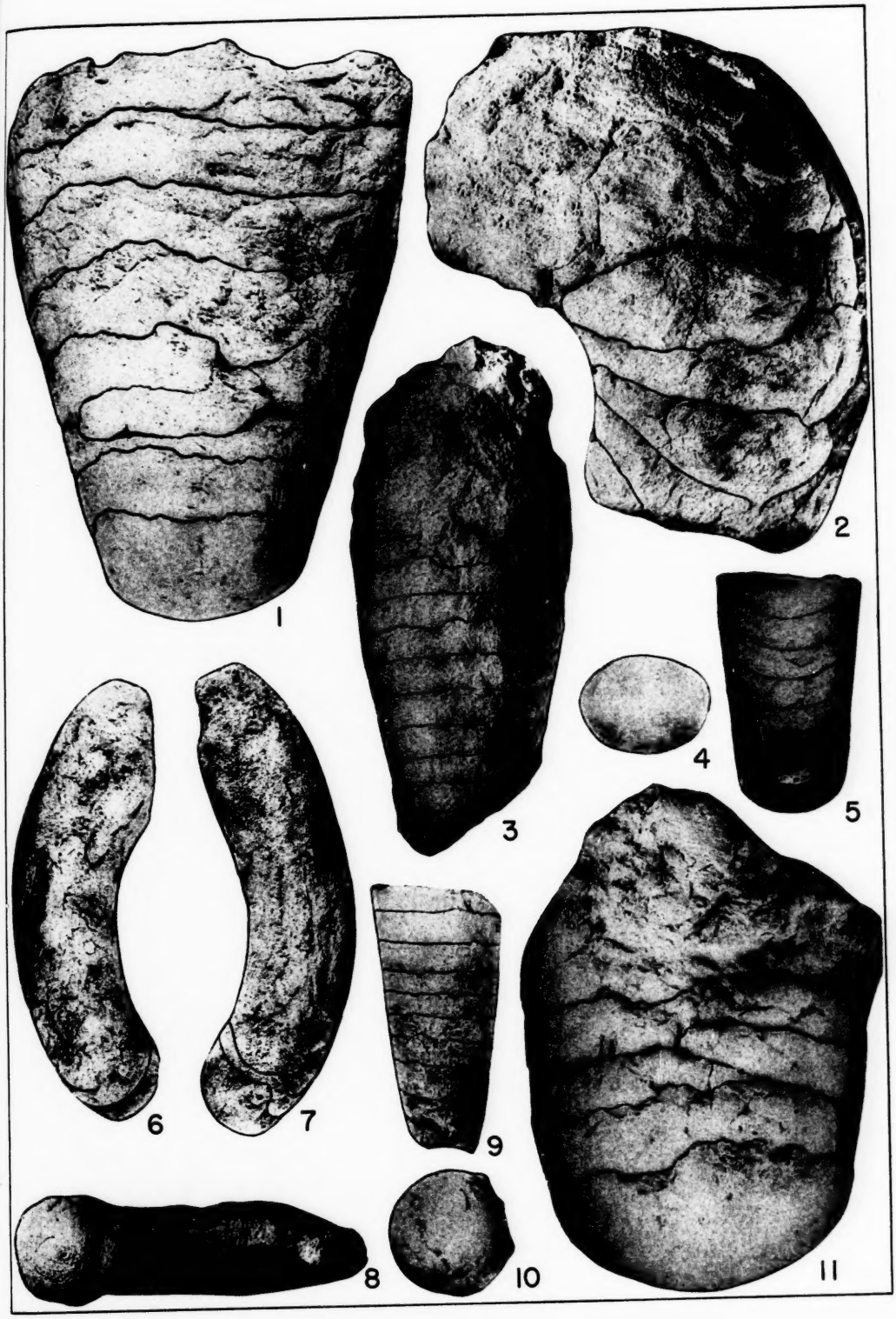
EXPLANATION OF PLATE 143

All specimens illustrated are from the Rockford limestone of Jasper County, Indiana, and are ×½. Photographs are retouched.

FIG. *1*—*Welleroceras liratum* Miller & Furnish. Lateral view.
*2*—*Aipoceras?* sp. Lateral view. Third chamber preserves position of siphuncle and size and shape of siphuncular neck.
*3*—*Poterioceras?* sp. Lateral view.
*4–5*—*Mooreoceras?* sp. *4*, End view to show elliptical transverse section and *5*, Natural longitudinal cross-section.
*6–8*—*Rineceras digonum?* (Meek & Worthen). Lateral and end views.
*9–10*—*Poterioceras?* sp. Lateral and end views.
*11*—*Poterioceras?* sp. Lateral view.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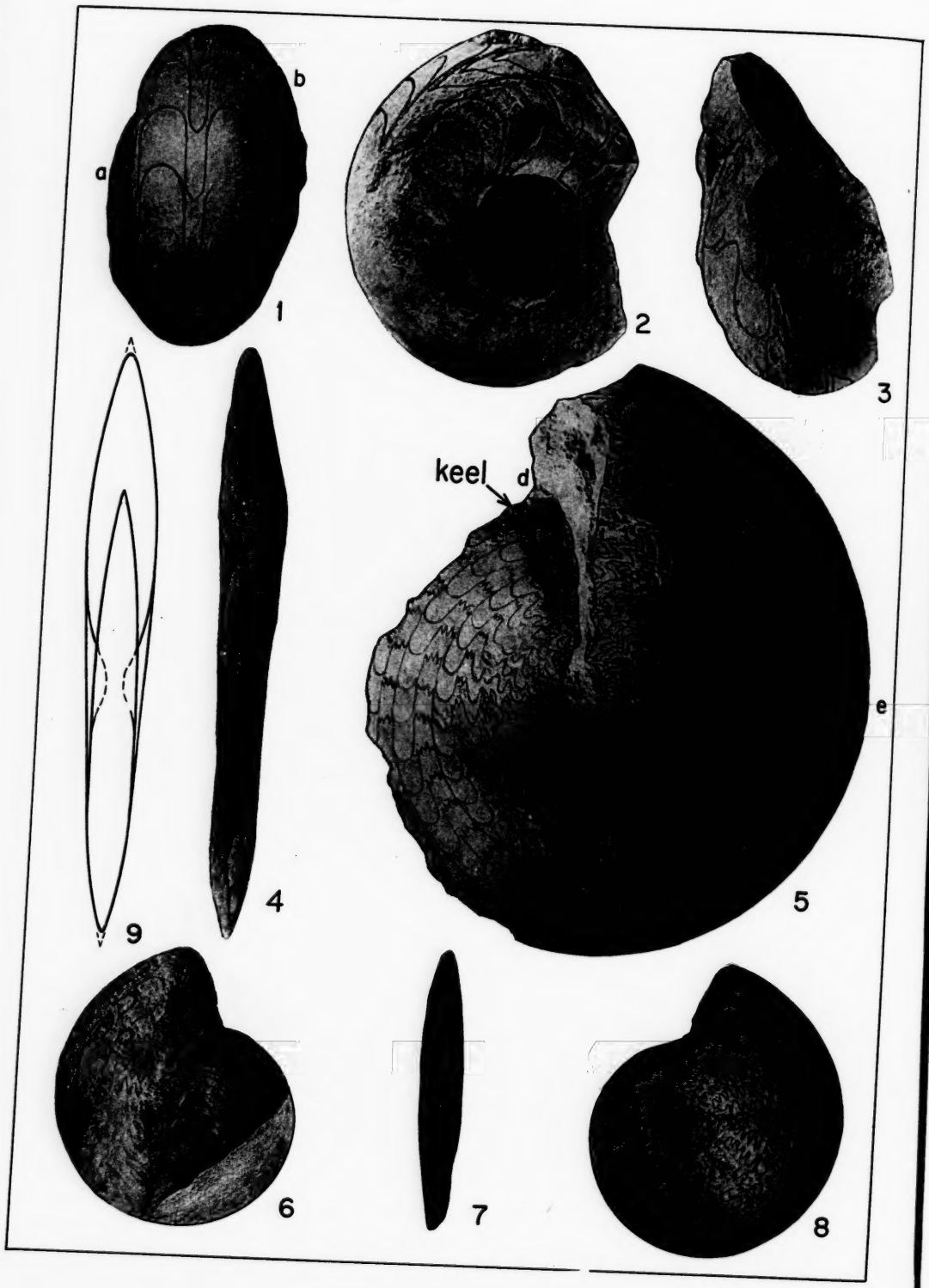
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*Poterioceras* ? spp.
Plate 143, fig. 3,9–11

There are three specimens in the collection which probably represent two species questionably referred to this genus. The two specimens illustrated by fig. 3,9 and 10 on Plate 143; closely resemble *Poterioceras northviewensis* of Missouri and *Poterioceras?* sp. of Michigan (Miller & Garner, 1953a, p. 184). The specimen illustrated by fig. 3 on Plate 143 is adorally compressed; whereas adapically it seems to be more circular in cross-section and with the smaller form could easily give a composite picture of the entire conch. The specimen shown by fig. 11 (on Pl. 143) does not closely resemble any described form of this genus; however, the nature of the specimen does not merit establishment of a new species.

*Mooreoceras?* spp.
Plate 143, fig. 4,5

There are four orthocones which are poorly preserved internal molds that lack any trace of the siphuncle. They vary from almost circular to elliptical in cross-section and undoubtedly represent more than one species. It is probable that the circular form is *Mooreoceras indianense* (Hall) originally described from the Rockford of southern Indiana. The forms with elliptical transverse sections, one of which is illustrated, may be closely related to similar ones described by Miller & Garner (1953a, p. 164–175) from the Marshall sandstone of Michigan.

*Subclass Ammonoidea*
Genus *Gattendorfia* Schindewolf

Identification of the genus is based upon the conclusions reached by Miller et al. (1951, p. 467; 1955, p. 120) in which they characterize the genus as having (1) umbilicus which is open and (2) undivided ventral lobe. *Gattendorfia*, *Imitoceras*, and *Münsteroceras* appear to be very closely related and may represent variations of the same form either in phylogenetic or ontogenetic development. The former two genera are very similar except for the umbilicus; whereas *Gattendorfia* and *Münsteroceras* are alike except for the character of the ventral lobe.

It is difficult to differentiate species within the genus *Gattendorfia* because most described American species are represented by single specimens some of which may be immature. As a result, uncertainties arise in evaluating suture patterns, umbilici, transverse constrictions, and other features.

*Gattendorfia alteri* Gutschick & Treckman, n. sp.
Plate 144, fig. 1–3; Text-fig. 3A–C

The single large specimen on which this species is based is a completely septate internal mold representing a little more than one-half the entire conch. The slightly distorted fossil is fairly well preserved in limestone. The subglobular conch is oval-shaped in transverse section and expands rapidly orad. The maximum diameter of this incomplete specimen measures about 85 mm.; however, the animal must have been much larger since the living chamber is not present.

The whorls are depressed dorsoventrally, broadly rounded ventrally and ventrolaterally, subangular dorsolaterally, and impressed dorsally. The maximum width of the whorl measures about 50 mm. and its height is close to one-half its width. The umbilicus which is partly filled with lime matrix appears to be open. It is moderately large, 28 mm., which is one-third the maximum diameter of the conch

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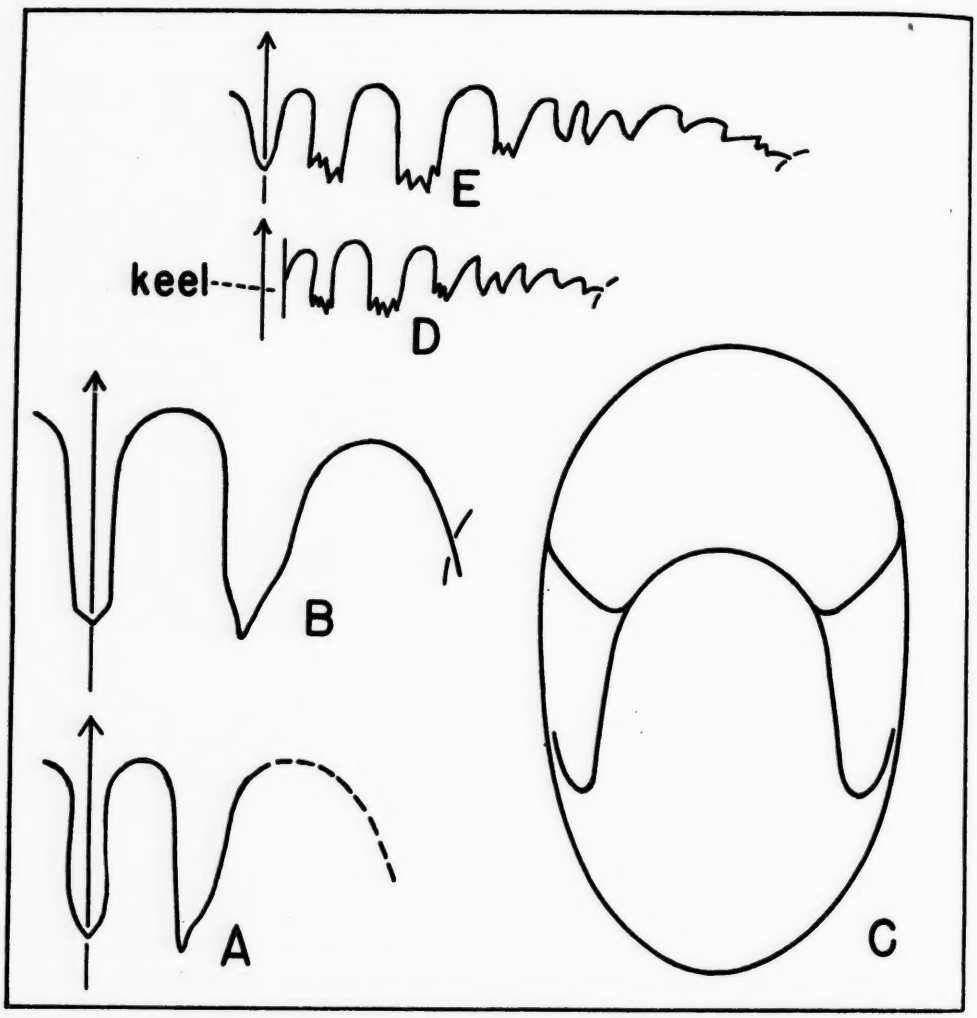
EXPLANATION OF PLATE 144

All specimens illustrated are from the Rockford limestone of Jasper County, Indiana, and are (×⅔). Photographs are retouched.

FIG. *1–3*—*Gattendorfia alteri* G. & T., n. sp. Three views of the holotype. *1*, Ventral view; a and b indicate position chosen for diagrammatic representation of suture patterns (Text-fig. 3A-B); *2*, lateral view—note faint lirae on remnants of shell around umbilicus; and *3*, ventral view showing cross-section of umbilical wall and shoulder.

*4–9*—*Prodromites gorbyi* (Miller). Lateral and ventral views of two specimens. *4* and *9*, Ventral views showing reconstruction of slightly crushed specimen; *5*, lateral view; d and e indicate position of suture diagram (Text-fig. 3D-E); and *6–8*, Three views of smaller specimen partly restored.




TEXT-FIG. 3—Diagrammatic suture drawings and cross-section (×1). A-C, *Gattendorfia alteri* n. sp., A. Suture pattern position indicated by (a) on pl. 144, fig. 1. B. Mature suture (b) on pl. 144, fig. 1. C. Diagrammatic reconstruction of transverse section; D-E, *Prodromites gorbyi*, D. Suture pattern (d.) pl. 144, fig. 5. E. Suture pattern (e.) pl. 144, fig. 5.

The umbilical shoulder is abrupt and subangular. The slightly convex umbilical walls make an angle of approximately 125° with the ventrolateral margin. Remnants of the shell along the umbilical shoulder display faint transverse lirae.

The ventral portion of the sutures is moderately well preserved. The shell is characterized by a narrow, deep, acutely pointed ventral lobe with pronounced parallel sides. The proximity of the lateral lines of succeeding ventral lobes accentuates the parallelism of these lines which are almost continuous around the venter. The first lateral saddle is U-shaped, followed by an acutely V-shaped first lateral lobe which is slightly longer than the ventral lobe. The second lateral saddle is symmetrical U-shaped disappearing beneath the shell inside the umbilical shoulder. The sutures along the dor-

sal margin are not visible nor is there any indication of a siphuncle. No transverse constrictions have been observed.

*Remarks.*—*Gattendorfia alteri* comes closest to resembling *G. bransoni* Miller & Youngquist (1947, p. 116) from the Caballero formation of New Mexico. The Rockford fossil is much larger in size. It has definite parallel-sided ventral lobes which closely resemble *Münsteroceras parallelum* except for the divided ventral lobe in the latter. In addition the first lateral lobe in *G. alteri* is longer than the ventral lobe. The slope of the umbilical walls are much less steep and the conch appears to be less compressed dorsoventrally than *G. bransoni*.

*Gattendorfia alteri* also resembles Miller & Garner's *G.* ? sp. of Michigan in general form, but the latter lacks preservation of the sutures for comparison. *Goniatites brownensis* Miller (1892, p. 700) is also similar. Miller & Garner (1955, p. 121) refer this species to *Gattendorfia* which seems reasonable; however, the original illustrations and description leaves much to be desired. The Indiana State Museum, which is supposed to have the holotype of *G. brownensis*, has been unable to locate the single specimen for comparison.

The specific name is given in honor of Mr. Chris E. Alter who collected and saved the specimen.

### *Prodromites gorbyi* (Miller)
Plate 144, fig. 4–9; Text-fig. 3D-E

Miller & Collinson (1951, p. 481) give an excellent detailed summary of more than thirty specimens of this monotypic genus along with a redescription of the holotype. Since only two specimens seem to be known from the Rockford limestone of southern Indiana, it was decided to illustrate and comment on the four specimens in this collection especially in view of the excellence of the two illustrated. The others are well preserved portions of large phragmocones comparable in size to the large illustrated form. All fossils are completely septate internal molds. The maximum diameter of the large figured specimen, lacking the living chamber and keel, measures 148 mm. The keel is exfoliated except for the small segment along the adapical part of the last whorl. The fossils are essentially free of matrix, partly crushed on one side, and have a well preserved suture pattern. The specimen shown on Plate 144, figs. 6–8, is similar to the holotype of "*P. praematurus*" [=*P. gorbyi*] which has also come from the Rockford limestone.

*Prodromites gorbyi* is now known from southern and northern Indiana, southeastern Iowa, western Illinois, common in Missouri but has not been reported from Michigan or Ohio.

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JOURNAL OF PALEONTOLOGY, VOL. 31, NO. 6, P. 1154–1158, PL. 145–148, NOVEMBER 1957

# BITHECAE, GONOTHECAE AND NEMATOTHECAE ON GRAPTOLOIDEA

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ABSTRACT—A study with high magnification shows that bithecae, gonothecae, and namatothecae are characteristically developed on Upper Cambrian dendroid graptolites of Virginia and Tennessee, and a similar study by means of higher magnification shows the presence of bithecae, gonothecae, and nematothecae on the stipes of numerous species in the various genera of *Graptoloidea*.

The significance of these structures is discussed, the names of species bearing them are listed, their importance in helping to determine placement in the animal kingdom is noted, and photographic enlargements of them are shown on accompanying plates.

## INTRODUCTION

IN ADDITION to autothecae, bithecae have been recognized generally as characteristic of dendroid graptolites. Recently, the writers found that in addition to these two types of thecae, gonothecae and nematothecae are present not only on Cambrian dendroid graptolites, but also on Ordovician, Devonian, and Mississippian species of this branching group.

Bulman (1938, p. 38) tells of the presence of bithecae in *Clonograptus tenallus* and *Bryograptus hunnebergensis*, and implies that bithecae have been lost at various in-

### EXPLANATION OF PLATE 145

All illustrations are unretouched photographs by Irwin B. Gold.

FIG. *A1,2—Didymograptus sagitticaulis* Gurley
*1*, Stipe, ×2; *2*, small part of stipe, ×25; (*n*), nematothecae, and (*p,p*), two preserved polyps with nematothecae on them where periderm of thecae is exfoliated. Stringtown shale, a mile east of Atoka, Oklahoma.

*B1,2—Dicellograptus forchammeri flexuous* Lapworth
*1*, Part of stipe, ×2; *2*, part of stipe, ×28, showing theca at (*t*) with nematothecae around aperture, and (*p*), polyp with nematothecae protruding. Viola limestone, 4 miles southwest of Bromide, Oklahoma.

*C1,2—Dicellograptus gurleyi* Lapworth
*1*, Colony, ×3.5; *2*, part of colony, ×28; *S*, point of sicula with hive-shaped gonotheca on its lower part at (*g*), a second gonotheca up at left at (*g*), regular theca above *t*. Athens shale, a half mile east of Pratts Ferry Bridge, Alabama.

*D1,2—Dicellograptus intortus* Lapworth
*1*, Large part of colony, ×2; *2*, part of stipe, ×28, showing gonothecae (*g*), broken thecal polyp at (*p*), and bithecal polyp at (*b,p*). Athens shale, a half mile east of Pratts Ferry Bridge, Alabama.

*E—Diplograptus crassitestus* Ruedemann
Part of stipe, ×26, showing thecae at (*t*), broken thecal polyp above at right with large gonothecal polyp to left of it, and broken bithecal polyp at (*b,p*), and nematotheca at (*n*). Sylvan shale, Lawrence quarry, south of Ada, Oklahoma.

### EXPLANATION OF PLATE 146

All illustrations are unretouched photographs by Irwin B. Gold.

FIG. *A—Diplograptus crassitestus* Ruedemann
Part of stipe, ×28, showing ends of two polyps protruding with nematothecae on them at (*p*), with aperture at right closed and at left open; and with nematocyst extending at *n*. Sylvan shale, Lawrence quarry, south of Ada, Oklahoma.

*B—Diplograptus calcuratus alabamensis* Ruedemann
Part of stipe, ×40, showing two thecal polyps *p*, two bithecal polyps at *b,p*; and gonotheca above *g*. Athens shale, one mile south of Bristol, Tennessee.

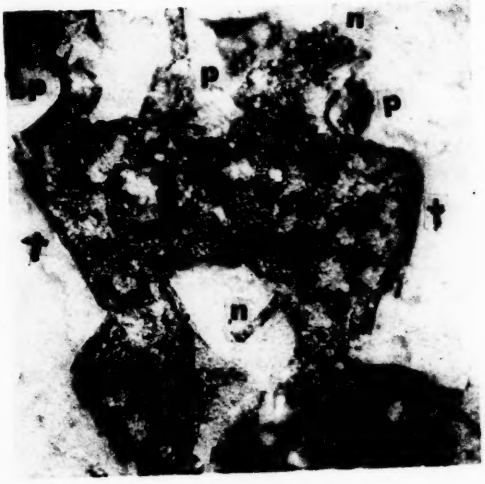
*C1,2—Diplograptus truncatus* Lapworth
*1*, Stipe, ×2; *2*, part of stipe, ×17, showing gonotheca above (*g*), and bitheca above (*b*). Womble shale, 0.1 mile east of Crystal Springs, Arkansas.

A

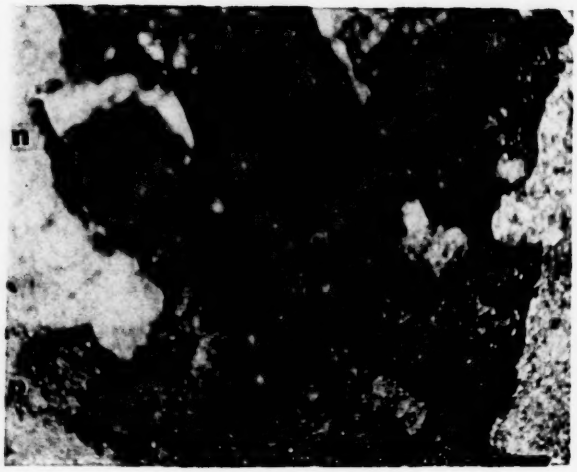
1 B 2

C

D

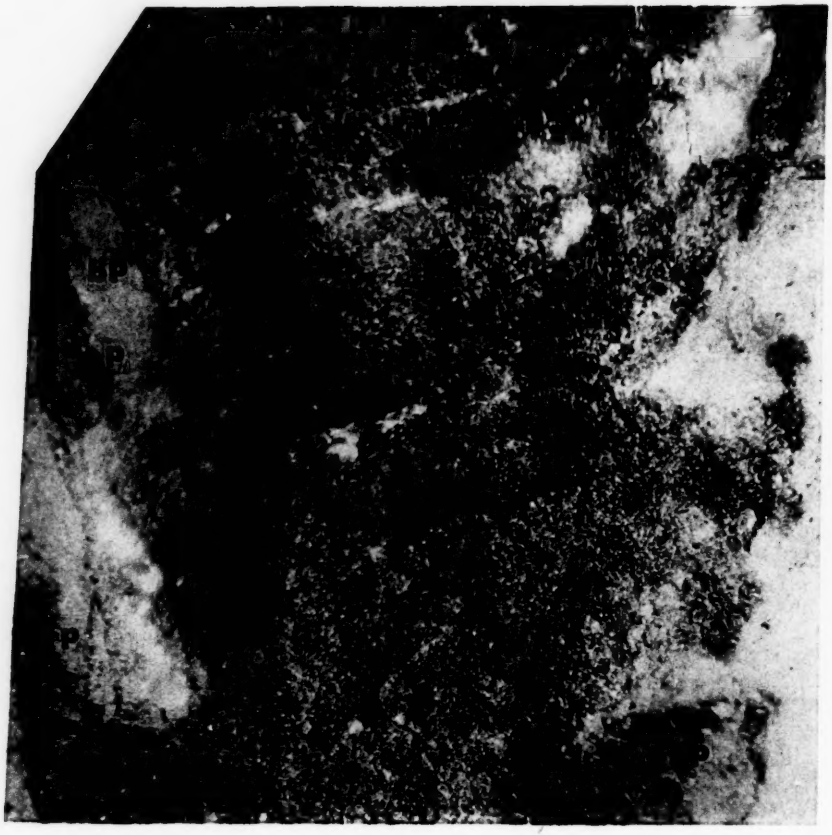



E



A

1 C 2



B

A 2

B

1 2 C

2 D 1

A 2

B

2 C 1

D 2

tervals by all other graptoloid species.

Recent studies by the writers show that not only do bithecae occur on the stipes of numerous species of graptoloids, but also that many slender bithecal polyps have been preserved on them. Also, numerous hive-shaped gonothecae occur on these stipes, and this structure representing the female element, together with bithecae, satisfies the requirement for bisexual reproduction. This does away with the idea that autothecae might serve as the female elements.

Also, the writers have found that tiny nematothecae to house stinging cells are characteristic of the various groups of both dendroid and graptoloid species, thus having the protective structures so characteristic of members of the coelenterate group.

A most important discovery has been made in finding numerous thecal and bithecal polyps and a few gonothecal polyps with a single row of extensible tentacles around the aperture and with nematothecae around the free part of the body, as well as on the thecae and along the stipes. The bithecal polyp is smallest, being long and slender, the autothecal polyp is intermediate in size, and the gonothecal polyp is the largest and is barrel-shaped.

*Species Listed*

The structures mentioned above are represented on 14 different species or subspecies from eight formations. The names of the species or subspecies are as follows:

*Didymograptus sagitticaulis* Gurley
*Dicellograptus forchammeri flexuosus* Lapworth
*Dicellograptus gurleyi* Lapworth
*Dicellograptus intortus* Lapworth
*Diplograptus crassitestus* Ruedemann
*Diplograptus calcaratus alabamensis* Ruedemann
*Diplograptus truncatus* Lapworth
*Climacograptus bicornis* (Hall)
*Climacograptus scharenbergi* Lapworth
*Climacograptus typicalis* Hall

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EXPLANATION OF PLATE 147

All illustrations are unretouched photographs by Irwin B. Gold.

FIG. *A1,2—Climacograptus bicornis* (Hall)
*1*, Part of stipe, ×3.5; *2*, part of stipe, ×28, showing gonotheca to left of (*g*) and nematothecae at (*n*). Viola limestone, West Branch Sycamore Creek, Sec. 27, T. 35 N., R. 4 E., southeast of Sulphur, Oklahoma.

*B—Climacograptus scharenbergi* Lapworth
Part of stipe (×28) showing bitheca at *b* and two gonothecae to the left and right of (*g*), Stringtown shale, Latimer County, Oklahoma.

*C1,2—Climacograptus typicalis* Hall
*1*, Stipe, ×2; *2*, part of stipe, ×26, with theca (*t*), gonotheca at (*g*), and polyp at (*p*). Eden (Trenton), near Sulphur Springs, Kentucky.

*D1,2—Glossograptus quadrimucronatus spinigerus* Lapworth
*1*, Part of stipe, ×2; *2*, part of stipe, ×17, with theca at (*t*), gonothecae (*g*), bithecae (*b*), and nematothecae at (*n*). Viola limestone, Rock Crossing, Criner Hills, Oklahoma.

EXPLANATION OF PLATE 148

All illustrations are unretouched photographs by Irwin B. Gold.

FIG. *A1,2—Lasiograptus eucharis* (Hall)
*1*, Most of a stipe, ×4; and *2*, a large part of a stipe, ×17. On *A2* a dark hive-shaped gonotheca is shown at lower left with light aperture, a theca on each side at (*t*, *t*), a nematotheca below (*n*) on the right, and several near the middle of the stipe below (*n*), a slender bithecal polyp on the right above (*p*), and a large barrel-shaped gonothecal polyp on lower right at (*p*).

*B—Lasiograptus eucharis* (Hall)
Part of stipe, ×17, with hive-shaped gonotheca (*g*), and barrel-shaped gonothecal polyp at (*p*).

*C1,2—Monograptus vulgaris* Wood
*1*, stipe, ×2; *2*, part of stipe, ×26, partly exfoliated with theca at (*t*), bitheca at (*b*), and bithecal polyp at (*b*, *p*). Henryhouse shale, Cool Creek, Sec. 36, T. 2 S., R. 1 E., Oklahoma.

*D1,2—Monograptus marri* (Perner)
*1*, stipe, ×2; *2*, part of stipe, ×28, with polyp at (*p*) showing single row of extended tentacles around aperture. Gala-Tarrannon beds, Middle Silurian, Czechoslovakia.

*Glossograptus quadrimucronatus spinigerus* Lapworth
*Lassiograptus eucharis* (Hall)
*Monograptus vulgaris* Wood
*Monograptus marri* (Perner)

Of the 14 graptoloid species listed above, five are illustrated on Plate 145, which also includes a *Didymograptus*, three *Dicellograptus* and *Diplograptus*. Most extensiform, or horizontal, *Didymograptus* occur in the Lower Ordovician; the species illustrated occurs in the Athens shale of Trenton age. The two horizontal thecae shown at the top of figure *A2* on Plate 145 have part of the thecal wall exfoliated, exposing the ends of two calcified polyps, *p* with nematothecae showing on the surface, and a nematotheca showing on the stipe below *n*.

On Plate 145 three *Dicellograptus* are illustrated. Figure *B2* shows a theca at *t* and a calcified polyp with nematothecae at *p*. Figure *C2* illustrates a theca above *t*, an end of a sicula at *s* and two gonothecae at *g,g*. On figure *D2*, the upper end of a broken polyp is at *p*, a bithecal polyp with nematothecae at *bp*, and a hive-shaped gonotheca at *g*. On the distal end of *Diplograptus crassitestus* illustrated by figure *E*, two thecae are shown at *t,t;* at the upper right, a calcified polyp labeled *p* has nematothecae showing at *n* with a larger gonothecal polyp to the left of *n* and to the right of *p;* a bithecal polyp is at the upper left and to the right of *b,p*.

Plate 146, figure *A*, shows an enlargement (×28) of the middle part of the same stipe of *Diplograptus crassitestus* as that shown on Plate 145, figure *E*. On the right, the closed end of a polyp with nematothecae shows at *p*, on the left part of a polyp protrudes from the thecal aperture with nematothecae around the aperture and on its sides at *p*, and a nematotheca shows above it at *n*. Also, two other species of *Diplograptus* are shown by figures *B* and *C*. At the bottom, figure *B*, part of a stipe of *Diplograptus calcaratus alabamensis* is enlarged (×40) with two thecal polyps preserved on the left at *p,p;* higher up a bithecal polyp with nematothecae on it shows at *b,p;* on the lower right another bithecal polyp shows at *b,p;* a hive-shaped gonotheca with light aperture shows above *g*.

At the upper right above figure *C*, *Diplograptus truncatus* is shown ×2 in *1*, and ×17 above *2*, where a gonotheca occurs above *g* and a smaller bitheca above *b*.

Three species of *Climacograptus* and a *Glossograptus* are shown on Plate 147. A part of a stipe of *Climacograptus bicornis* near the tapering proximal and is shown ×35 in figure *A1* and ×28 in figure *A2*. In figure *A2*, two large hive-shaped gonothecae are shown, one at the left of *g* and a darker one higher up. Nematothecae are perserved on the two upper thecae at the right near *n* and *n*. *Climacograptus scharenbergi*, figure *B*, shows three large hive-shaped gonothecae, two marked from *g* on the left side and one marked from *g* on the right; a bithecal aperture is at the left of the upper *b*, and part of a bithecal polyp is preserved to the left of the lower *b*. *Climacograptus typicalis* is shown ×2 by figure *C1*, and part of a stipe (×26) is illustrated by figure *C2*. In figure *C2*, a theca shows at the left of *t*, a large hive-shaped gonotheca is to the right of *g*, and a bithecal polyp is to the lower right at *p*.

Parts of a broad stipe of *Glossograptus quadrimucronatus* are shown on Plate 147, ×2 and ×17, figure *D1* and *D2*, respectively. Two thecae are marked at the right and left of *t,t;* gonothecae to the right of *g,g* on the left side, and to the left of *g* on the upper right; and nematothecae are preserved on the apertures of two thecae on the right at *n* and *n*, and below *n* and *n* in the middle of the stipe.

On Plate 148 two stipes of a species of *Lasiograptus* and a part of a stipe of two species of *Monograptus* are illustrated. A large part of a stipe of *Lasiograptus eucharis* is illustrated ×4 by *A1* and ×17 by *A2*. On *A2* a dark hive-shaped gonotheca with white aperture is shown at lower left to the right of *g*, thecae are shown to the right and left of *t* on both sides of the stipe, a nematotheca shows to the left at *n* on the aperture of a theca, and several nematothecae show below *n* near the middle of the stipe; on the right side a slender bithecal polyp is shown above *p* and a barrel-shaped gonothecal polyp on lower right at *p*. Part of a stipe of *Lasiograptus eucharis* is shown ×17 above *B*, with a large light colored hive-shaped

gonotheca at *g*, and with a large dark barrel-shaped gonothecal polyp with open aperture protruding out of the gonothecal aperture at *p*. Part of a stipe of *Monograptus vulgaris* is shown ×2 by *C1* and ×26 by *C2*. On *C2* there is a theca at *t* with nematothecae around the aperture; and high at right a nematotheca below *n;* a bitheca below *b* and a bithecal polyp at *b* and *p*. *Monograptus marri* is shown ×2 by *D1* and ×28 by *D2*. On *D2* a polyp is preserved with a single row of extensible tentacles around the aperture above *p*.

Many of the various structures shown on the plates are preserved in great detail and they give significant information concerning the habits and characteristics of the graptolite polyps, and the newly discovered reproductive and protective structures give important evidence concerning graptolite affinities.

Until recently, graptolites were commonly placed under Coelenterata. However, Kozlowski (1948) completed his study of fragmental Ordovician graptolites of southern Poland, and found in them a stolonal canal and fusellar structure in the periderm of graptolites, similar to those in *Rhabdopleura*, and so, in his otherwise excellent work and without giving due consideration to the many basic differences between graptolites and *Rhabdopleura*, he made the terrible mistake of placing graptolites with *Rhabdopleura* under Hemichordata.

Not being familiar with the new clear-cut evidence of reproductive and protective structures discovered recently by the writer as characteristic of all groups of graptolites throughout their history from Cambrian through Mississippian, and fearing that Bulman might follow Kozlowski, the writer urged that he should not make this marked change in the classification of graptolites; yet he did make the change. Then the authors of two new editions of textbooks of invertebrate paleontology followed him using many of Kozlowski's illustrations.

These new editions were by (1952) Moore, Lalicker and Fischer, *Textbook of Invertebrate Fossils*, p. 715–732, and by Shrock and Twenhofel, (1953) *Principles of Invertebrate Paleontology*, p. 736–757.

In response to an article on *The Place of Graptolites in the Animal Kingdom* in which the writer (1956) gave outstanding reasons why graptolites should not be classed under hemichordates, statements of complete agreement with the writer have been received from prominent geologists, paleontologists, and biologists, and Abbie Hyman of the American Museum of Natural History has stated that she is leaving graptolites out of volume IV on Hemichordata in her invertebrate series, and she asked the writer to give the reasons why graptolites should not be classed with Hemichordata.

The marked change in classification was made on the evidence of two structures in graptolites, a stolonal canal and fusellar structure in the periderm similar to those in *Rhabdopleura*, but the force of the argument for this change was lessened by the finding of fusellar structure in blastoid and worm-like forms.

The chief differences between graptolites and *Rhabdopleura* are as follows: Three basic structures characteristic of graptolites, siculae, bithecae, and nematothecae are absent in *Rhabdopleura*. Graptolites had rigid stipes with great regularity in positions and number of thecae, while *Rhadopleura* has flexible zooidal tubes irregularly arranged.

Graptolites had a tubular digestive system with a single row of extensible tentacles around the oral aperture, while *Rhabdopleura* has a U-shaped digestive system with anal opening adjacent to the oral aperture above which two plume-like structures are covered with tentacles.

Many species of graptolites with floating habit attained world-wide distribution, while *Rhabdopleura* remains cemented to the bottom of the ocean.

The adaptive graptolites developed hundreds of new species and varieties, while *Rhabdopleura* forms a dead-end group with little power to develop new species. *Rhabdopleura* is placed under Hemichordata because it possesses gill slits and a rudimentary notochord, a condition far removed from graptolites with their simple digestive system and numerous stinging cell structures so characteristic of the Coelenterata.

The new evidence concerning the structure and parts of the graptolite polyps, and

especially the high development of stinging cells in all graptolite groups, seems to relate them closely to the *Coelenterata* under which they may be placed as a very specialized class, as suggested by Birger Bohlen (1950).

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JOURNAL OF PALEONTOLOGY, VOL. 31, NO. 6, P. 1159–1166, 5 TEXT-FIG., NOVEMBER 1957

# THE ARTHROPOD SPECIES *ANTHRAPALAEMON DUBIUS* AND RELATED FORMS

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ABSTRACT—British specimens of *Anthrapalaemon dubius* show differences from those described from other areas. The general form, size, raised central area, ornamentation, cervical furrows and anterior and lateral spines are discussed in detail. The taxonomic value of these and other characters is considered. It is suggested that a number of molt stages may be represented by the various sizes of carapace. It appears that *A. dubius* was nonmarine and that *A. grossarti* was also very probably nonmarine in its habitat. *A. dubius* occurs from the *Lenisulcata* to the *Similis-Pulchra* zone in Britain. The status of other species of the genus is discussed.

## INTRODUCTION

THE genus *Anthrapalaemon* was erected by Salter in 1861 to include a group of malacostracan arthropods from the Upper Carboniferous of Britain. The genus has subsequently been found in Upper Carboniferous strata from other localities in Britain as well as in Nova Scotia, the United States, France, Belgium, Holland and Germany. About thirty papers have been written concerning the genus. Six species with two varieties are currently recognized, although Van der Heide (1951) has recently suggested that only three species are actually represented by these described specimens. At least one of the species, *A. dubius*, appears to be of stratigraphic value.

The recent discovery by the writers of this species in the Upper Carboniferous of Northern England has led us to study all the specimens available in England. This has provided new information concerning the morphology, stratigraphic range and relationships of the species.

We are greatly indebted to Dr. C. J. Stubblefield, F.R.S., for his kindly critical interest, and to Dr. H. W. Ball and Mr. M. A. Calver for their courtesy in allowing us access to the collections at the British Museum (Natural History) and the Geological Survey, London, respectively, and for their generous help and advice. Mr. Calver has given much assistance with the stratigraphic problems encountered. Dr. Van der Heide of the Geologische Stichting, Haarlem, Netherlands, has kindly provided us with information about the specimens which he described from the Limbourg basin.

## SYSTEMATIC PALEONTOLOGY

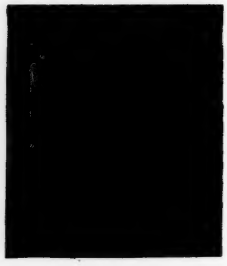
Phylum ARTHROPODA
Subclass MALACOSTRACA
Order SCHIZOPODA
Family LOPHOGASTRIDAE
Genus ANTHRAPALAEMON Salter, 1861

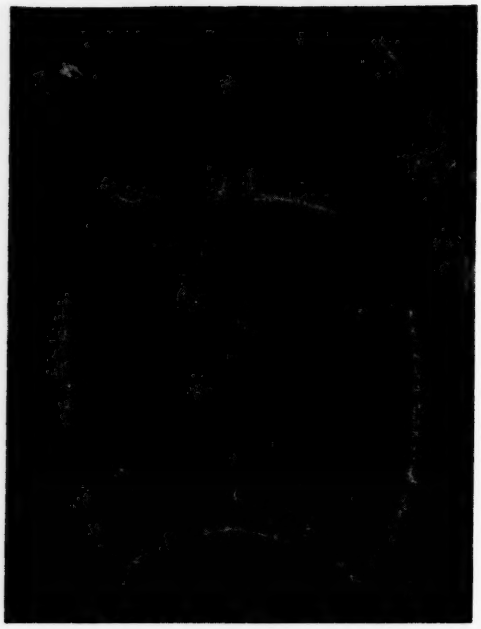
Type species: *A. grossarti* Salter.

*Anthrapalaemon* SALTER, 1861, Quart. Jour. Geol. Soc., London, vol. 17, p. 529; MEEK & WORTHEN, 1865, Phila. Acad. Nat. Sci., Proc., vol. 17, p. 50; ——, 1866, Illinois Geol. Surv., Paleont., vol. 2, p. 406; H. WOODWARD, 1877, Geol. Soc. Glasgow, Trans., vol. 2, p. 55–56; PACKARD, 1885, Amer. Naturalist, vol. 19, p. 880; PEACH, 1908, Roy. Soc. Edinburgh, vol. 30, p. 29–30; VAN DER HEIDE, 1951, Med. Geol. Sticht., ser. C-IV-3, no. 5, p. 26–39.
*Palaeocarabus* SALTER, 1863, Quart. Jour. Geol. Soc., London, vol. 19, p. 521.

### ANTHRAPALAEMON DUBIUS (Milne-Edwards)
Text-fig. 1—1–3

*Apus dubius* MILNE-EDWARDS, 1840, *in* Prestwich, pl. 41, fig. 9.
*Anthrapalaemon* (*Palaeocarabus*) *dubius* SALTER, 1861, Geol. Soc. London, Trans., ser. 2, p. 532, fig. 6 and 7.
*Palaeocarabus russellianus* SALTER, 1863, Quart. Jour. Geol. Soc. London, vol. 19, p. 520, fig. 1 and 2.
*Anthrapalaemon grossarti* WOODWARD, 1866, Geol. Soc. Glasgow, Trans., vol. 2, p. 244, pl. 3, fig. 5–7; ——, 1877, (part), Brit. Mus., Cat. Brit. foss. Crustacea, p. 8; JONGMANS, 1928, Med. Geol. Bur. Ned. Mijngebied, no. 6, pl. 17, fig. 5; PRUVOST, 1930, Mus. Roy. Hist. Nat. Belg., Mém. 44, p. 179, pl. 10, fig. 4; RENIER, ET AL., 1938, Mus. Roy. Hist. Nat. Belg., Flore et Faune houillères de la Belgique, p. 199, fig. 76; VAN DER HEIDE, 1946, Med. Geol. Sticht., ser. C-IV-3, no. 4, p. 39, pl. 1, fig. 18 and 19; DALINVAL, 1948, Soc. géol. Nord. Ann., t. 67, p. 27, fig. 1; non! SALTER,





TEXT-FIG. *1*—*Anthrapalaemon dubius* (Milne-Edwards). *1*, Dorsal surface of specimen from Tynemouth, Northumberland (catalogue number: B1a, Durham Colleges), showing complete anterior margins before excavation of the rostrum, approx. ×1.8. *2*, Obverse side of matrix from which specimen B1a was extracted (catalogue number: B1b, Durham Colleges), approx. ×2.6. *3*, Dorsal surface of specimen showing rostrum (catalogue number: B1a, Durham Colleges), approx. ×4.8.

1861, Geol. Soc. London, Trans., ser. 2, p. 530, fig. 1–4.

*Anthrapalaemon Hilliana* Dawson, 1877, Geol. Mag., vol. 4 p. 56, fig. 1.

*Anthrapalaemon glaber* JONES & WOODWARD, 1899, ibid., p. 393, pl. 15, fig. 5.

*Anthrapalaemon russellianus* PEACH, 1908, Mem. Geol. Surv. Gt. Brit., pl. 4, fig. 1–6.

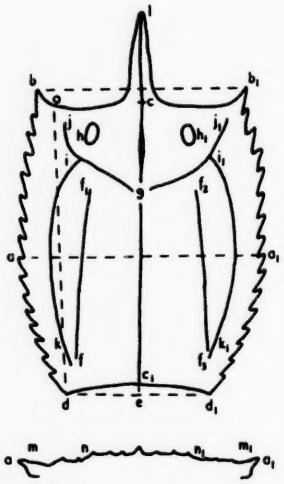
*Anthrapalaemon russillianus* var. *spinulosus* PEACH, 1908, ibid., pl. 36, fig. 7.

*Anthrapalaemon hillianus* BELL, 1922, Roy. Soc. Canada, Proc. and Trans., ser. 3, vol. 16, p. 162, pl. 1, fig. 10.

*Anthrapalaemon* of. *russellianus* DIX, 1930, The Naturalist, p. 103.

*Anthrapalaemon dubius* VAN DER HEIDE, 1951, Med. Geol. Sticht., ser. C-1V-3, no. 5, p. 26–39, pl. 3, fig. 4,5; pl. 4, fig. 2–10; pl. 5, fig. 1–11; pl. 6, fig. 1–5; PAPROTH & SCHMIDT, 1955, Paleont. Zeitschr., vol. 29, p. 83–86, fig. 1.

A revised diagnosis and a description of this species have been given by Van der



TEXT-FIG. *2*—Diagrammatic representation of *Anthrapalaemon dubius*. The upper figure is a dorsal view and the lower a median transverse section. The following dimensions and morphological features are shown:

| | |
|---|---|
| $aa_1$ | greatest breadth |
| od | length |
| $cc_1$ | length (along dorsal ridge) |
| b and $b_1$ | anterior lateral spines |
| d and $d_1$ | posterior lateral angles |
| $c_1e$ | depth of posterior notch |
| cl | rostrum |
| f $f_1$ $f_2$ $f_3$ | outer limit of raised central area |
| bad and $b_1a_1d_1$ | lateral (ventral) margins |
| g | cervical furrow |
| h and $h_1$ | gastric elevations |
| i $i_1$ | points of bifurcation of cervical furrow |
| ij and $i_1j_1$ | anterior prongs of cervical furrow |
| ik and $i_1k_1$ | posterior portions of cervical furrow |
| n $n_1$ | outer margins of raised central area (which displays strong ornamentation) |
| m $m_1$ | marginal areas (no ornamentation) marginal to posterior portions of cervical furrows |

Heide (1951, p. 27–29), who also made a careful review of the literature (1951, p. 29–34). Since the present writers accept Van der Heide's opinions regarding the synonomy of the species, our purpose here is to supplement Van der Heide's description of the carapace by the additional information afforded by the British specimens. The morphological terms used in the following discussion are illustrated in Text-figure 2 and are referred to in the text by small letters [e.g. dorsal ridge = ($gc_1$)].

*Dimensions.*—Van der Heide measured the length of specimens from the "posterior notch" to the "anterior border" (personal communication, 1956). During the present study the length was measured from the postero-lateral angle (d and $d_2$) to the anterior margin at the base (o) of the anterior spine (b and $b_1$) on the same side of the carapace. This gives a value closely comparable with the length as understood by Van der Heide. In crushed specimens our measurements may exceed that given by Van der Heide by about ½ mm.

It will be noted from Table I that the British specimens are generally slightly larger than those described by Van der Heide (1951) from Limbourg. The British fossils are also very slightly broader in relation to length. Table I compares measurements for a fauna from the most prolific British locality (Cossall Clay Pit, Nottinghamshire), with the measurements given by Van der Heide (1951). When other miscellaneous British specimens are also included, the limits of the species *A. dubius* must be modified to include forms having a maximum length of 28 mm., a maximum breadth of 27 mm., a minimum length of 6.5 mm. and a minimum breadth of 6.5 mm. The dimensions of these forms are shown in Text-figure 5. The holotype of *A. dubius* (Milne-Edwards *in* Prestwich, 1840) is the largest recorded specimen of the species.

*The Rostrum* (cl).—This structure is usually flattened and sometimes poorly preserved. In well preserved specimens it appears to be sub-triangular in cross-section, with the dorsal mid-line being marked by a sharp carina. The carina extends posteriorly onto the carapace until it is interrupted by the cervical furrow (g). Posterior to this it is continued as a dorsal ridge ($gc_1$) which, although it may be partly obliterated by post-depositional distortion, extends to the posterior margin of the carapace.

*The raised central area* (f, $f_1$, $f_2$, $f_3$).—In the majority of specimens—including both the holotype and the second specimen described (Salter, 1861)—the central portion of the carapace is prominently raised above the level of the marginal area. This central area is terminated laterally by two more or less conspicuous edges, lying within and subparallel to the posterior prongs of the cervi-

TABLE I—DIMENSIONS OF SPECIMENS OF *Anthrapalaemon dubius* (FOR EXPLANATION SEE TEXT).

| | Dimensions in mm. for specimens from Cossall Clay Pit, Nottinghamshire | | | | | Dimensions in mm. of specimens from Limbourg given by Van der Heide (1951) | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Minimum | Maximum | Norm | Number of Specimens | Observed Range | Minimum | Maximum | Norm | Number of Specimens |
| Length ($cc_1$) | 10.0 | 22.0 | 16.5 | 14 | 12.0 | 5.5 | 24.0 | 15.5 | 100+* |
| Breadth ($aa_1$) | 9.0 | 22.0 | 16.7 | 14 | 13.0 | 5.31 | 23.2 | 15.0 | |
| Length ($cc_1$) / Breadth ($aa_1$) | | | 0.99 | 14 | | | | 1.04 | |
| Length of rostrum (cl) | 6.0 | 12.5 | 8.80 | 14 | 6.5 | 5.0 | 14.5 | 9.8 | |
| Length ($cc_1$) / Length of rostrum (cl) | | | 1.89 | 14 | | | | 1.58 | |
| Number of lateral spines | 13 | 18 | 15 | 14 | 5 | 9 | 15 | 11 | |
| Density of ornamentation | 120 | 360 | 204 | 14 | 240 | 75 | 425 | 219 | |

* Van der Heide, personal communication, 1956.

TEXT-FIG. 3—Variation in the number of lateral spines on the carapace of *Anthrapalaemon dubius*. Black = specimens from Cossall clay Pit, Nottinghamshire. Crosshatch = other miscellaneous British specimens. Van der Heide (1951) gives 9 as the minimum, 15 as the maximum, and 11 as the mean number of lateral spines. He does not include the total frequency in his data.

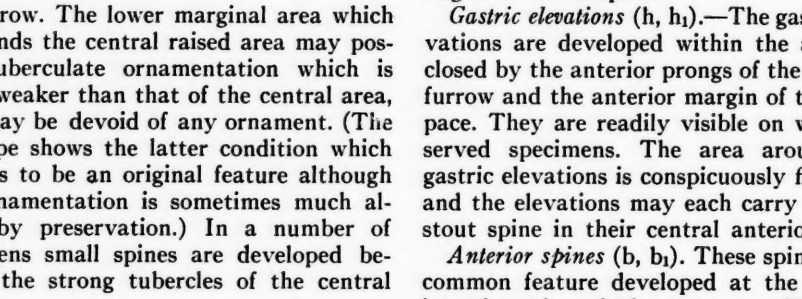
cal furrow. The lower marginal area which surrounds the central raised area may possess tuberculate ornamentation which is much weaker than that of the central area, or it may be devoid of any ornament. (The holotype shows the latter condition which appears to be an original feature although the ornamentation is sometimes much altered by preservation.) In a number of specimens small spines are developed between the strong tubercles of the central area.

*Cervical furrows* (jik, $j_1i_1k_1$).—These furrows are among the most constant features of all the British specimens of the species, although they may be partly obliterated by crushing of the carapace. The furrow extends outwards from, and on each side of, the cervical fold, which it intersects at a distance of about one-third the length of the carapace from the anterior margin. It is more or less indented and is directed from the cervical furrow towards the antero-lateral margins. At points i and $i_1$, situated approximately midway between the dorsal ridge and the margins of the carapace, the furrow bifurcates.

The anterior prongs (kj, $i_1j_1$) extend in a curving line on each side of the dorsal ridge towards the anterior margin of the carapace. The less conspicuous posterior prongs (ik, $i_1k_1$) are recurved in the opposite direction and extend almost to the postero-lateral angles of the carapace.

*Gastric elevations* (h, $h_1$).—The gastric elevations are developed within the area enclosed by the anterior prongs of the cervical furrow and the anterior margin of the carapace. They are readily visible on well preserved specimens. The area around the gastric elevations is conspicuously flattened and the elevations may each carry a single stout spine in their central anterior areas.

*Anterior spines* (b, $b_1$). These spines are a common feature developed at the antero-lateral angles of the carapace. They are usually conspicuous, stout, straight, bluntly




TEXT-FIG. 4—Variation in density of ornamentation in specimens of *Anthrapalaemon dubius*. Crosshatch = miscellaneous specimens in collection of H. M. Geological Survey and the British Museum (Natural History). Black = specimens in collection of H. M. Geological Survey from Cossall Clay Pit, Nottinghamshire.

pointed flattened spines, directed anteriorly and laterally.

*Lateral spines* (d, $d_1$).—The numbers of spines developed along the lateral margins of the carapace shows some variation in the British specimens. Text-figure 3 shows this variation and a comparison of it with that recorded by Van der Heide for specimens from Limbourg. The British specimens carry more spines on the whole than the Dutch ones. The spines are invariably directed antero-laterally and show varying degrees of spinosity. This latter feature apparently depends to some extent, however, upon the preservation. The spines along the posterior portions of the lateral margins are less frequently preserved, probably because they stand erect to the carapace. The spines may also decrease in size posteriorly.

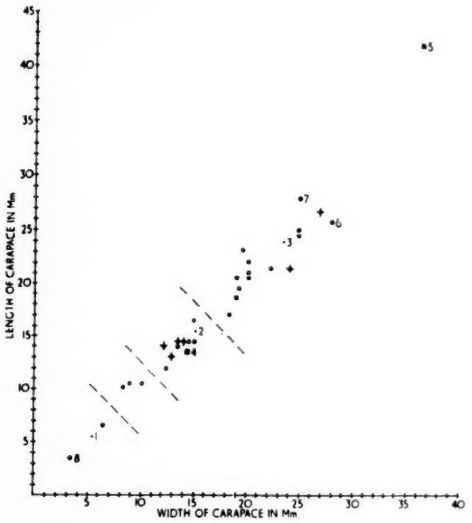
*Ornamentation.*—The ornamentation of the carapace is one of the most variable features in this species. The difference between the ornamentation of the raised central area and that of the marginal areas has already been discussed. The general variation in ornamentation affects both the distribution and the size of the tubercles. The density of their distribution is quite variable, even for specimens of similar size. This is illustrated in Table I and Text-figure 4.

The density of ornamentation on various parts of the carapace may not be uniform. The measurements plotted are all for the raised central area. The comparison with Van der Heide's data shows some variation between the British and Limbourg specimens, although Van der Heide writes (personal communication, 1956) that where "the density of the ornament has been measured on the whole carapace, it is extremely variable."

In a few specimens the spines are of variable size, secondary spines being developed among the primary. The ornamentation of specimens is much influenced by the state of preservation.

*Depth of posterior notch* ($c_1e$).—This has been considered by some writers to be of diagnostic value. The present specimens indicate, however, that its dimensions are very largely dependent on flattening and other distortion. In uncrushed specimens it is very shallow.

*Molt stages.*—Figure 5 indicates that there is a barely discernible grouping of the various specimens plotted on the Length-Breadth graph. This is tentatively interpreted as indicating that the specimens represent a series of molt stages. The fact that only the larger specimens are found associated with fragments of antennae, antennules, body segments and telson plates may be an indication that these represent dead adults rather than molt stages, the appendages having become separated from the carapace in fossil specimens of younger molts. Alternatively the appendages of




TEXT-FIG. 5—Variation in length and width of carapace for specimens of *Anthrapalaemon dubius*.

1. Minimum dimensions of *A. dubius* described by Van der Heide (1951).
2. Mean dimensions of Van der Heide's specimens of *A. dubius*.
3. Maximum dimensions of Van der Heide's specimens of *A. dubius*.
4. Specimen from Tynemouth, North Point, Northumberland.
5. *A. holti*, holotype.
6. *A. grossarti*, holotype.
7. *A. dubius*, holotype.
8. Small *A. grossarti*.

Broken lines indicate possible molt stages.

● Miscellaneous specimens in collection of H. M. Geological Survey.

○ Specimens in collection of H. M. Geological Survey from Cossal clay pit, Nottinghampshire.

\+ Specimens in collection of British Museum (Natural History).

these younger molts may be less "calcified" than the older, and therefore unrepresented as fossils. The close similarity in form and ornament throughout the size range of the specimens is a striking feature.

### COMPARISON OF A. DUBIUS WITH OTHER SPECIES

Both *A. holti* and *A. grossarti* are plotted on Figure 4. It will be noted that *A. grossarti* shows little size difference from specimens of *A. dubius*. The difference between the density of ornamentation in the two forms is, however, very striking. The maximum for any specimen of *A. grossarti* is 400 tubercles per sq. cm., while that for the holotype of *A. grossarti* is 2,000, and that for the only other specimen of that species studied is 10,000 (this latter is the very small form shown on Table 4). This finely granulose ornamentation is quite distinct from that of *A. dubius* and covers all the dorsal surface of the carapace, apart from the areas marginal to the posterior prongs of the cervical furrows.

Van der Heide (1951, p. 33) regards the absolute size difference between *A. holti* (Woodward, 1911) and *A. dubius* as the diagnostic difference between the two supposed species. Comparisons indicate, however, that the difference between the holotype of *A. dubius* (which is admittedly somewhat atypical of the species) and the holotype of *A. holti* is less than that between the holotype of *A. dubius* and small specimens of that species.

The holotype of *A. dubius* is larger than any other known specimen of the species, has fewer lateral spines than most specimens studied, and has a smaller density of ornamentation.

### PALEOECOLOGY

Van der Heide (1951, p. 37) has recently noted that *A. dubius* from Limbourg is always found in nonmarine strata, in general being rare in beds containing nonmarine pelecypods and more common in those containing ostracods (especially *Limnoprimitia*). The most common faunal association of the British specimens is with nonmarine pelecypods and plants. Ostracods and *Spirorbis* are more rarely found in association with the species. Specimens are usually preserved in dark grey or black, compact, brittle, fissile shales or more rarely in pale grey shales. Numbers of other specimens, including the holotype, are preserved in chalybite nodules.

The faunal and sedimentary associations of the British specimens support the view that *A. dubius* was a nonmarine creature.

In striking contrast to this it is generally assumed that *A. gossarti* was marine in its habitat (e.g., Van der Hiede, 1951, p. 37). The chief evidence for this rests on the observation by Salter (1861, p. 529) that the holotype was associated with *Lingula*, *Conularia* (?) and fish. The holotype is preserved in dark shale which is indistinguishable from that in which most specimens of *A. dubius* are preserved. The back of the specimen shows a fossil plant. The horizon from which it was collected is probably in the vicinity of the Halifax Hard Bed Coal (or its Scottish equivalent). At one locality (9 ft. above the Sough Coal, spoil heap at Newman's Spinney open cast site near Spink Hill, 1.5 miles N.N.W. of Barlborough, Derbyshire) *A. dubius* and *A. grossarti* are both found, and probably come from the same horizon. It thus appears that *A. grossarti* was probably also nonmarine in its habitat.

### GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION OF ANTHRAPALAEMON IN BRITAIN

In general the stratigraphic distribution of *Anthrapalaemon* in Britain corresponds with that recorded by Van der Heide (1951, p. 34–35). It is most prolific in the lower *Modiolaris* Zone of Nottinghamshire and has also been recorded from the top of the *Lenisulcata* Zone, to the *Similis-Pulchra* Zone.

The known occurrences of the species are as follows:

*Mid-lower Similis-Pulchra Zone*

| | |
|---|---|
| Palace Craig Black Band | Glasgow Coalfield (Salter 1863) |
| 9 ft. above Sough Coal | Open cast site near Spink Hill, 1½ miles N.N.W. of Barlborough, Derbyshire |
| Crow Coal (probably equivalent to the Brass Thill Seam) | Phoenix Brickworks, Crawcrook, near Ryton-on-Tyne, Durham |

| | |
|---|---|
| *Upper Modiolaris Zone* | |
| Soft Band Ironstone | Greengairs, 3.5 miles N.N.E. of Airdrie, Lanarkshire (Peach, 1908) |
| Lidgett Bed | Oxclose, Scholes, Nr. Rotherham, Yorkshire |
| White Flat Ironstone | Coalbrookdale, Shropshire. (This is the holotype of the species: Catalogue no. G.S.M. S4398–9) Prestwich (1840) |
| Mushett's Black Band Ironstone | Chapel Hill, Airdrie (Woodward 1867). |
| Soft Band Ironstone (below Airdrie Blackband) | Stream section E. of S. of crossroads at Greengairs, 3½ miles N.N.E. of Airdrie, Lanark |
| Probable roof of Plessey Seam | Tynemouth North Point, Northumberland |
| *Lower Modiolaris Zone* | |
| 33 ft. below Clay Cross Marine Band | ? |
| Roof of Piper Coal | Cossall Clay Pit, Nottinghamshire |
| 92′ depth below surface | Borehole at Whitehaven laundry, Cumberland |
| *Lower Modiolaris—Top Communis Zone* | |
| 12 ft. above Cannel Coal | Sinking at Cefn-y-Coed Colliery, 4½ miles S.S.E. of Mold Station, Flintshire |
| Between Deep Hard and Silkstone Coals | Bondsmain Colliery, Temple Normanton, Derbyshire |
| *Leninsculata Zone* | |
| Slaty band of Blackband Ironstone | Goodhock Hill, Shotts, Lanarkshire Salter (1861) |

### NOTES ON OTHER RECORDED SPECIES OF ANTHRAPALAEMON

*Anthrapalaemon couttsii* Peach manuscript (Coutts, *in* Patton, 1885, p. 327) was reported from two localities (Limekilns Quarry and Kirkonholm Mines) in the Calderwood Group of the Lower Limestone Series of East Kilbride, Lanarkshire. Patton (p. 322) notes that fossils from the first of these localities are from strata connected with the Calderwood Limestone and Calderwood Cementstone. The fauna and flora from this locality include typical coal measure plants, foraminifers, sponges, corals, echinoderms, annelids, crustaceans, polyzoans, brachiopods, molluscs and fish.

Coutts (1885, p. 214) exhibited specimens of *Anthrapalaemon* from the "cement-limestone shales of East Kilbride" before the Glasgow Geological Society in 1882. He believed the specimens to represent new species of the genus. It is not clear whether or not these specimens represent the same ones as those later identified by him as *A. couttsii*.

Peach (1908, p. 59) refers to *Palaemysis couttsi* as being collected by Andrew Patton from the same locality. The specimens were submitted to Peach by Coutts. It appears possible, therefore, that Peach's unillustrated and undefined manuscript species of *Anthrapalaemon*, was removed by him to to the genus *Palaemysis*.

*Anthrapalaemon parkeri* H. Woodward, 1907. Woodward named (but did not describe) this species from specimens occurring in clay ironstone nodules in shales of the Middle Coal Measures at Sparth Bottoms, half a mile southwest of Rochdale Town Hall, in beds estimated to occur 135 feet above the Royley Mine Coal-seam (1907, p. 568).

The work of Peach (1908) and Van Straelen (1931) suggests that the following species should be transferred from the genus *Anthrapalaemon:*

*A. etheridgei* Peach (1881) to *Teallocaris*
*A formosus* var. *latus* Peach (1881)
*A. macconochiei* Etheridge (1879) to *Pseudogalathea*
*A. ornatissimus* Peach (1881) to *Pseudogalathea*
*A. parki* Peach (1881) to *Perinectherus*
*A. traquairi* Peach (1881) to *Anthracophansia*
*A. woodwardi* Etheridge (1877) to *Teallocaris*

Packard (1886, p. 139) regarded the sketch of a specimen provided by McCoy, which was figured by Salter (1861, fig. 5) and tentatively referred by him to *Anthrapalaemon*, as representing a distinct genus, *Archicaris*.

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# CRETACEOUS AMMONITES FROM EASTERN APACHE COUNTY, ARIZONA

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ABSTRACT—A small collection of ammonites from the lowest member of the Mesaverde formation in Apache County, Arizona, contains *Metoicoceras*, *Calycoceras*, and *Dunveganoceras* (?) in association with *Exogyra columbella* Meek. These ammonites indicate that the lowest Mesaverde in this area is Lower Turonian or perhaps even Upper Cenomanian in age.

## INTRODUCTION

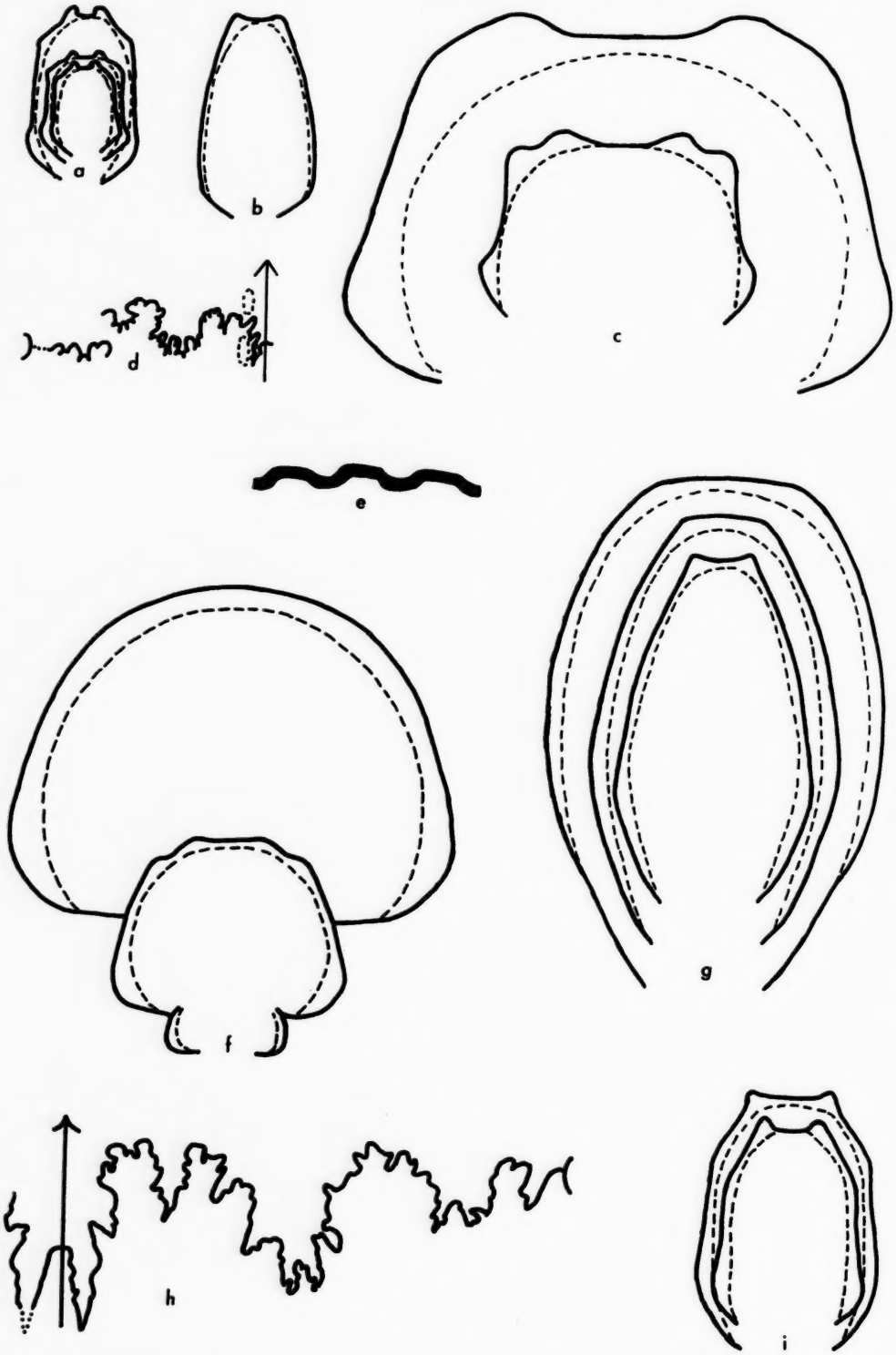
SOUTHWEST from the San Juan Basin the base of the Mesaverde formation drops rather rapidly by replacing the Mancos shale, as admirably illustrated by Sears, Hunt, & Hendricks (1941), W. S. Pike (1947), and others. The lower part of the Mesaverde formation has been illustrated as Middle Turonian in age by Cobban & Reeside (1952), Pike (1947), and others, in the Datil region, west-central New Mexico: It has been shown to include rocks of Upper Turonian age in the southern San Juan Basin by Reeside (1924), Burton (1955), Dane (1946), and others. In the Black Mesa area, northeastern Arizona, the lower Mesaverde has also been shown to include rocks equivalent in age to at least part of the Upper Turonian (Ross, 1915; Cobban & Reeside, 1952; Repenning & Page, 1956).

Recent work by graduate students of the University of Texas (O'Brien, 1956) in the area east of Saint Johns, Arizona, indicates that the base of the Mesaverde drops even lower, probably into equivalents of the Upper Cenomanian. According to O'Brien (1956, p. 33) the "Dakota" in this area consists of a lower sandstone, a middle shale (which may be thin or entirely absent), and an upper sandstone; the three parts totalling 45 to 65 feet. Above this there are approximately 300 feet of strata between the top of the "Dakota" and the base of the Atarque member of the Mesaverde formation. These 300 feet consist, in ascending order, of approximately 100 feet of shale, designated Mancos by O'Brien (1956, p. 38); 90 feet of sandstone, considered the basal unit of the Mesaverde formation by O'Brien (1956, p. 40–41); and 125 feet of sandstone and sandy shale.

The fossils, some of which are described later in this paper, were collected from the top 20 feet of the unnamed sandstone unit which O'Brien considered to represent the basal unit of the Mesaverde formation. Therefore, the fossils are from 70 to 90 feet above the base of his Mesaverde. The fossils were collected from measured section number 8 of O'Brien (1956, p. 43–44), $\frac{1}{8}$ mile west of the New Mexico-Arizona state line (east boundary of sec. 3, T. 10 N. R. 31 E.), and $\frac{3}{8}$ mile south of the north boundary line of sec. 3, T. 10 N., R. 31 E., eastern Apache County, Arizona; from just below the basalt bed which caps a small ridge about $\frac{1}{8}$ mile east of the road through Summer's Valley.

In addition to the fauna discussed in the later paragraphs, at a slightly lower level in the Mesaverde-Mancos complex of this area various fragments of ammonites were found; these are unidentifiable but appear to be forms of *Kanabiceras* and *Eucalycoceras*. Detailed collecting in this area would probably provide a more nearly complete fauna.

The fossils described in the present paper were collected by R. K. DeFord, F. W. Rutledge, L. J. Rehkemper, T. D. Crutcher, and Bob R. O'Brien in the summer of 1955. Present information indicates that it is either Lower Turonian or Upper Cenomanian in age. It seems to be near the Cenomanian-Turonian boundary. Arkell, Kummel, & Wright (1957) show *Metoicoceras* to be Lower Turonian in age and *Dunveganoceras* to be Upper Cenomanian in age. They occur together in the present faunule, but the *Dunveganoceras* can be ignored because they are such unusual forms, and their as-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signment is questionable. Wright (1956) discusses the age relationships of *Metoicoceras* and *Dunveganoceras* in more detail and suggests that the species of *Metoicoceras* reported with *Dunveganoceras* in North America really belong to his genus *Utaturiceras* (Wright, 1956; Stephenson's, 1955, *Tarrantoceras* has priority, but its type species, *T. rotatile* Stephenson, is for a different group, and I am not yet willing to commit *Utaturiceras* to synonymy). This view of Wright's certainly ignores Cobban's (1953) paper on the fauna from the Mosby sandstone of Montana. By no stretch of the imagination can *Metoicoceras mulleri* Cobban or *M. mosbyense* Cobban be transferred to *Utaturiceras* Wright, even though they occur with undoubted species of *Dunveganoceras* (e.g., a subspecies of the type species of the genus).

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## SYSTEMATIC PALEONTOLOGY

Class CEPHALOPODA
Order AMMONOIDEA
Suborder AMMONITINA Hyatt, 1889
Superfamily ACANTHOCERATACEAE Hyatt, 1900
Family ACANTHOCERATIDAE Hyatt, 1900
Subfamily METOICOCERATINAE Hyatt, 1903
Genus METOICOCERAS Hyatt, 1903

METOICOCERAS DEFORDI Young, n. sp.
Pl. 149, fig. 1–8; Text-fig. 2—a,e,g,i

Oligogyral, excentrumbilicate, angustumbilicate in early whorls (up to shell diameters of 125 mm.), narrowly subangustumbilicate beyond shell diameters of 125 mm., craterumbilicate in earliest whorls. The whorl section is high and narrow throughout all observable whorls, presumably inflated in the nepionic stage, overlapping to the umbilical shoulder, with umbilicus expanding until the overlap is only to the midflank at a diameter of 175 mm. The intercostal section is rounded ventrally at all stages and the height/width ratio varies from 1.6 to 1.9 at diameters of 25 mm., increasing to almost 2.00 at diameters of 100 mm., then decreasing again as the umbilicus expands to about 1.7 at a diameter of 175 mm. The costal section shows considerable variation during the ontogeny, the two most ventral tubercles remaining high and pronounced to diameters of greater than 100 mm., thence the venter is tabulate to near diameters of 125 mm., becoming rounded at diameters of 150 mm. and larger. True ventro-lateral nodes are not present beyond the 40 mm. diameter, but the shape of the shell leaves a swelling that shows up in the whorl section, even though it does not photograph well (Text-fig. 1—i and Pl. 149 fig. 6,8). At diameters of 50 mm. the ribs do not cross the venter, but by a diameter of 75 mm. the ribs, though still bearing ventral clavae and umbilical bullae, cross the venter, rib height on the venter increasing with decrease in height of the clavae.

The ventral nodes are clavate throughout from a 20 mm. diameter on, whereas the ventro-lateral tubercles are nodated to the 40 mm. diameter where they begin to disappear. The umbilical nodes are extremely bullate, extending for the first third to the first half of the flank. The umbilical

TEXT-FIG. 1

*a, e, g, i—Metoicoceras defordi* Young, n. sp. *a*, whorl sections of UT 19785 at diameters of 25, 30, and 40 mm. (Pl. 149, fig. 3–5); *e, i*, two parts of holotype, UT 19786, *e*, sections of ribs from venter of large fragment and *i*, whorl sections at diameters of 50 and 77 mm. (Pl. 149, fig. 1,6, and 8); *g*, whorl sections of UT 18465 at diameters of 100, 125, and 175 mm (Pl. 149, fig. 2 and 7); all figures ×1; basal Mesaverde formation, eastern Apache County, Arizona.

*c—Dunveganoceras* (?) sp. A and B. Whorl sections of UT 18466A and UT 18466B, ×1 (Text-fig. 2—2–4); basal Mesaverde formation, eastern Apache County, Arizona.

*b, d—Metoicoceras* sp. *b*, whorl section of UT 18460 at a diameter of 53 mm., and *d*, suture of same individual at a diameter of 53 mm.; both ×1; basal Mesaverde formation, eastern Apache County, Arizona.

*f, h—Calycoceras obrieni* Young, n. sp. *f*, whorl section of holotype, UT 18469, at a diameter of 115 mm.; *h*, suture of same individual at a diameter of 100 mm. (Pl. 150, fig. 1–4); both ×1; basal Mesaverde formation, Apache County, Arizona.

bullae are the most pronounced of the three rows of nodes up to a diameter of 100 mm.; at larger diameters they are distinct to the body chamber on which they are effaced, remaining as ribs.

| | D | V | H | W | H/W | P | S | T |
|---|---|---|---|---|---|---|---|---|
| UT 19786 holotype | 75.0 | 16.0 | 50.5 | 30.0 | 1.69 | 8 | 22± | 30± |
| | 50.0 | 11.0 | 53.0 | 33.0 | 1.60 | | | |
| UT 19785 | 50.0 | 15.0 | 52.0 | 27.0 | 1.92 | | | |
| | 35.0 | 17.5 | 54.5 | 34.5 | 1.58 | | | |
| | 25.0 | 11.5 | 58.0 | 36.0 | 1.72 | | | |
| UT 18465 | 175.0 | 23.0 | 42.0 | 25.0 | 1.68 | | | |
| | 125.0 | 14.5 | 48.0 | 25.0 | 1.93 | | | |
| | 100.0 | 11.0 | 50.5 | 25.5 | 1.98 | | | |

At a diameter of 50 mm. the rib density consists of about 27 ribs per volution, increasing to approximately 30 ribs per volution at a diameter of 75 mm., and increasing to 35 or 36 ribs per volution at a 175 mm. diameter. Prior to the body whorl about a quarter of the ribs reach the umbilicus with umbilical bullae; a few may bifurcate, but most are secondary and intercalating.

Only a small section of the body whorl is preserved on specimen UT 18465, and the larger fragment of UT 19786 is a fragment of the body chamber. The last septum occurs at about a diameter of 135 mm. on UT 18465. UT 19786 was a little smaller at the same stage.

At a diameter of about 150 mm. the shell is about 0.7 mm. thick at the umbilicus, thickening ventrad to about 1.8 mm. ventrally. The fossils are all internal molds with a few fragments of shell adhering at small isolated localities, and no information can be acquired concerning the apertural features, even from growth lines.

It was not possible to recover a suture from any of the specimens. The suture illustrated in Text-fig. 1d is from a crushed specimen of unknown affinity, but does not seem to be *Metoicoceras defordi*, n. sp., because the umbilical bullae are retained only to a diameter of about 40 mm.

The measurements of three individuals follow: the letter symbols are those used by Young (1957).

*Remarks.*—*Metoicoceras defordi*, n. sp., was first thought to be related to *M. whitei* Hyatt (1903, pl. XIII, fig. 3–5), also illustrated by White as *M. swallovii*, but the rib sculpture is so different that the relationship cannot now be reconciled. Also, the two rows of ventrolateral nodes remain strong to much later diameters in *M. whitei*. If the accompanying meager information is correct, then *M. defordi* is considerably older than *M. whitei*. The rib sculpture of the adults (but not the young) of *M. defordi* is more like that of the much smaller *M. kanabense* Hyatt (1904), but at equivalent diameters the sculpture is entirely different. At comparable diameters, *M. defordi* is coarser ribbed and has much more bullate nodosity than does *M. kanabense*. The rib density of *M. defordi* compares with that of the larger specimens of *M. swallovii* in which rib density increases rapidly at a diameter of about 70 mm. (Stephenson, 1953 and Adkins & Lozo, 1951). *M. macrum* Stephenson and similar forms are more tumid with less dense ribbing at comparable diameters. *M. mulleri* Cobban (1953) also occurs with *Dunveganoceras* as does *M. mosbyense* Cobban (1953). The first of these species is so distinct from *M. defordi* that no further re-

PLATE 149

FIG. *1–8*—*Metoicoceras defordi* Young, n. sp. *2,7*, ventral and lateral views of UT 18465, the largest individual in the collection (Text-fig. 1g); *1,6,8*, two pieces of one individual, the holotype, UT 19786, lateral view of large fragment and ventral and lateral views of smaller fragment (Text-fig. 1); *3–5*, lateral and ventral views of UT 19785 (Text-fig. 1a); *2,7*, ×½; *1,3–6,8*, ×1.

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marks are necessary here. *M. mosbyense* is more delicately ribbed at diameters approaching 80 to 90 mm., and much more coarsely ribbed at diameters of 130 to 170 mm. than is *M. defordi.*

In *Metoicoceras ornatum* Moreman, *M. swallovii* (Shumard), and *M. gibbosum* Hyatt the two rows of nodes are maintained to greater diameters and the height/width ratio is less than in *M. defordi*, n. sp. *M. puercosense* Herrick & Johnson, 1900 is illustrated without strong costae and all ornamentation is effaced on the body whorl.

*Metoicoceras defordi*, n. sp., in whorl section and ornamentation appears to be related to *M. whitei* Hyatt, but the species is older than *M. whitei*, and the earlier disappearance of one pair of shoulder nodes and especially the flat topped ribs in the penultimate whorls and on the body whorls serve to separate the two species. The flat topped ribs would appear to be a specific specialization not transmitted to any younger known species of the genus.

*Types.*—UT 18786 (holotype), two fragments of the same individual, from the lower part of the Mesaverde formation, eastern Apache County, Arizona; Paratypes, UT 18465 and UT 19785, from the same locality and horizon as the holotype.

*Horizon and locality.*—Five individuals are known from the lower Mesaverde formation, eastern Apache County, Arizona.

Subfamily ACANTHOCERATINAE Hyatt, 1900
Genus CALYCOCERAS Hyatt, 1900
CALYCOCERAS OBRIENI Young, n. sp.
Pl. 150, fig. 1–4; Text-fig. 1—f,h

Oligogyral, concentrumbilicate, widely subangustumbilicate, gradumbilicate; whorl section compressed, overlapping to mid-flank (Text-fig. 1—f). The intercostal whorl section is reniform and more globular at earlier diameters, height/width ratio varying around 0.8; the costal whorl section is similar to the intercostal at the 100 mm. diameter, with bulges at the umbilicus where there are still large bullae; costal section more trapezoidal at earlier diameters because of the migration of the mediolateral bullae ventrally, a position more common in *Dunveganoceras* and *Paramammites* than in *Calycoceras.*

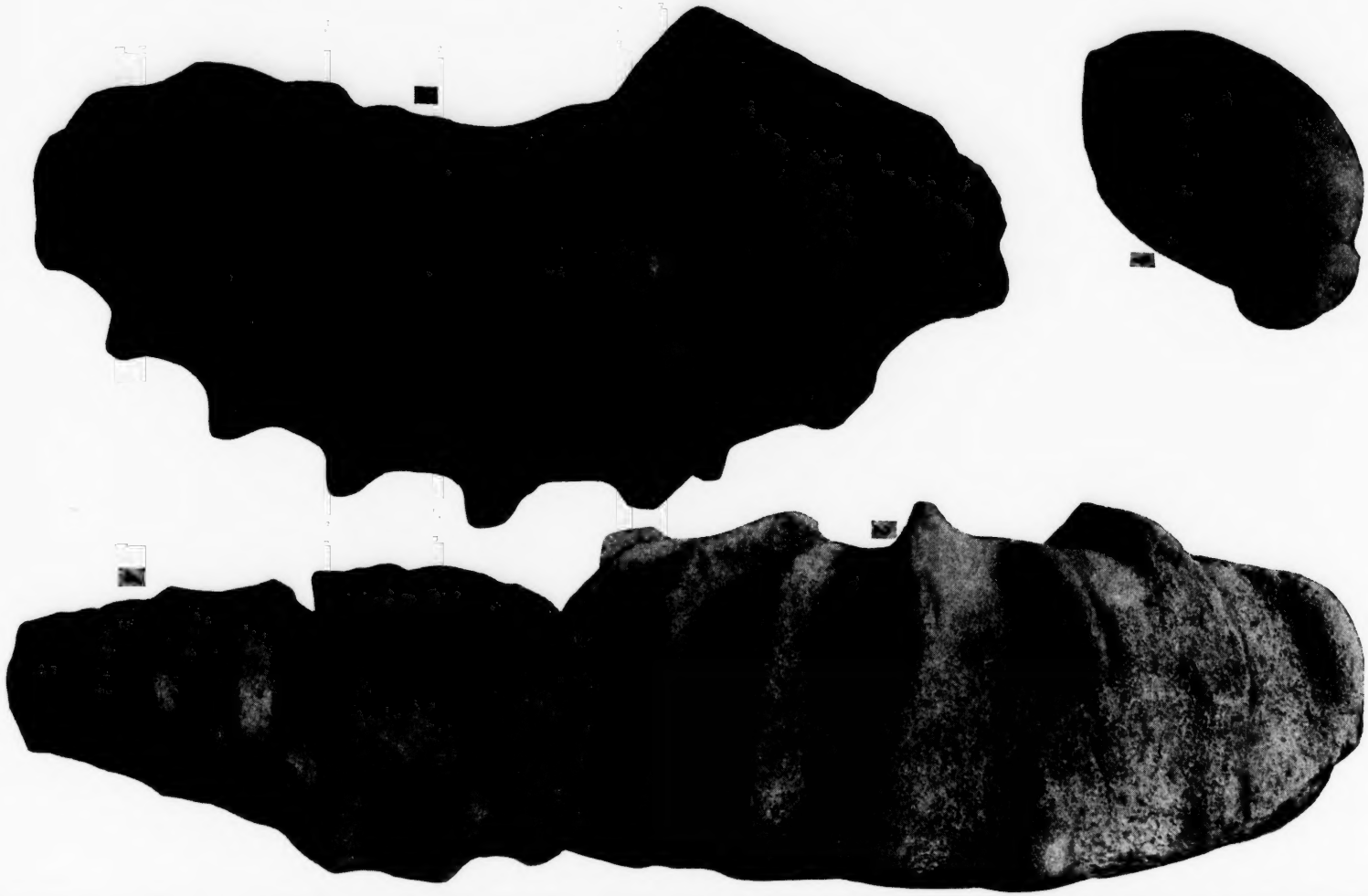
Adult costation is strong, there being 15 ribs on a half volution at a diameter comparable to that of *Calycoceras naviculare* (Mantell) at which the latter possesses 17 ribs, e.g., at a diameter of from 100 to 115 mm. At this stage very other rib is primary, extending to the umbilicus, the intervening secondary rib extending to mid-flank or just dorsad thereof. On the other hand, at a diameter of 50 mm. the appearance of the costation is less like that of *C. naviculare* (Mantell), the ribs being in groups of three on *C. obrieni*, n. sp., one primary rib and two secondary. The secondary ribs just orad and apicad of a primary rib may then extend almost to the umbilical bulla, or even join the umbilical bulla. At this stage there are approximately 8 primary ribs and 16 secondary ribs per volution.

Nodosity consists entirely of bullae at all observable diameters, the umbilical nodes being bullate throughout. The other nodes cannot be seen prior to the 40 mm. diameter. The taxonomic position of this species may be questionable because of the mid-line (ventral) ornamentation. At a diameter of about 40 mm. (and presumably prior thereto) there appears to be a very faint siphonal node, but by a diameter of 50 mm. this has been effaced and the rib is depressed at mid-venter; the depression may be the result of corrasion. The nodes, ventrolateral and mediolateral, are low and extremely bullate, the mediolateral displaced ventrad as early as the 40 mm. diameter. At diameters of 100 mm. the umbilical bullae are still pronounced and the ventrolateral bullae just visible. The mediolateral bullae and, of course, the siphonal nodes, are no longer present.

Very little can be said about the adult

PLATE 150

FIG. *1–4—Calycoceras obrieni* Young, n. sp. Ventral and lateral views of ultimate and penultimate whorls of holotype, UT 18469, septate throughout, ×1 (Text-fig. 1—f,h).



stage since the cast is septate throughout. The 115 mm. diameter whorl seems to have the coarse ribbing and the adult features of the genus. The body chamber is not preserved and apertural features are not known.

Few sutures of representatives of the genus of *Calycoceras* have been published. The suture of *C. obrieni*, n. sp., agrees reasonably well with that of *C. paucinodatum* (Crick) as figured by Collignon (1937, Pl. 14), but is more vascocerid, and is certainly not as acanthocerid as that of *Calycoceras stoliczkai* (Collignon), *C. obrieni* having a much more asymmetrical first lateral lobe.

The measurements of the holotype are as follows:

| | D | V | H | W | H/W | No. of ribs |
|---|---|---|---|---|---|---|
| UT 18469 | 115.0 | 33.0 | 41.0 | 53.0 | 0.77 | 14 ribs per half volution |
| | 100.0 | 27.0 | 45.0 | 54.0 | 0.73 | |
| | 50.0 | 28.0 | 50.0 | 61.0 | 0.81 | |

*Observations.*—In gross aspect *calycoceros obrieni*, n. sp., has the appearance of *C. naviculare* (Mantell) and the resemblance to figure 531–6 in Arkell, Kummel and Wright (1957) is remarkable. However, the youngest whorls are less similar, especially in the early loss of the siphonal node in *C. obrieni*. The whorl section is not as compressed as that of *C. stoliczkai* Collignon, and is more compressed than that of *C. paucinodatum* (Crick). *C. boulei* (Collignon) is more densicostate than is *C. obrieni*.

*Types.*—Holotype, UT 18469, from the lower part of the Mesaverde formation, eastern Apache County, Arizona.

*Horizon and locality.*—Basal Mesaverde formation, eastern Apache County, Arizona.

## Genus DUNVEGANOCERAS Warren and Stelck, 1940

### DUNVEGANOCERAS (?) sp. A

Text-fig. 1c, and Text-fig. 2.

Two new species of *Dunveganoceras* (?) bear illustration and description, but the specimens are insufficiently preserved to name. *Dunveganoceras* (?) n. sp. A is a fragment of an evolute body chamber in which the height/width ratio is considerably less than unity, unusual in species of *Dunveganoceras*. Costation is sparse, ribs being high, and steep, the intercostae about twice the width of the costae. The double shoulder tubercles are retained, but fused into one large bulla. The impressed zone on the dorsum shows the preceding whorl to have been densicostate with long bullae, intercostae equal to costae in width, each being about 2.3 mm. wide. This densicostate inner whorl precludes any possibility of *Dunveganoceras* n. sp. B described below being the juvenile of *Dunveganoceras* n. sp. A. The height /width ratio and the costation place this species in a different group from other *Dunveganoceras*, if the juvenile, when discovered, allows classification in this genus. The label of a similar individual in the Bureau of Economic Geology, from the Eagle Ford of North Texas, reads "*Calycoceras inequiplicatum* (Shumard)"; the label is in the writing of W. S. Adkins. I cannot accept a *Calycoceras* designation for either one of these individuals.

*Horizon and locality.*—Basal Mesaverde formation, eastern Apache County, Arizona.

### DUNVEGANOCERAS (?) n. sp. B

Text-fig. 1c, and Text-fig. 2

The unusual specimen figured here may be a *Dunveganoceras*. As in *Dunveganoceras* (?) n. sp. B the height/width ratio is consideraly less than unity. Costation is sparse, umbilical nodes bifurcating by extremely low costae to shoulder bullae with prominent nodes at each end. The fragment is

TEXT-FIG. 2

*1*—*Exogyra columbella* Meek. Fragmental individual from eastern Apache County, Arizona. This species here occurs in the lower Mesaverde formation with the fossils described in this paper.

*2–3*—*Dunveganoceras* (?) n. sp. A. Ventral and lateral views of part of body chamber of UT-18466A, ×1 (Text-fig. 1c, large whorl section).

*4*—*Dunveganoceras* (?) n. sp. B. Oblique ventral view of septate fragment, UT 18466B, ×1 (Text-fig. 1c, small whorl section).

septate, and the impressed zone is missing so that little more can be observed. Sutures not recoverable.

*Horizon and Locality.*—Lowermost Mesaverde formation, eastern Apache County, Arizona.

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JOURNAL OF PALEONTOLOGY, VOL. 31, NO. 6, P. 1175, NOVEMBER 1957

# PALEONTOLOGICAL NOTES

## SUPPLEMENTARY NOTES ON DEVONIAN CONODONT FAUNAS FROM SOUTHWEST ENGLAND

F. H. T. RHODES AND D. L. DINELEY
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The recent publication of our description of Devonian conodont faunas from southwestern England (1957) was printed without our having examined the galley proofs, and we could not include amendments made necessary by a number of recent papers published after the submission of the manuscript.

1. The species *Prioniodus idoneus* Stauffer should now be included within the genus *Neoprioniodus* (Rhodes & Müller, 1956). A *Neopriondus* from Limestone No. 1 was compared with this species (Rhodes & Dineley, 1957, p. 367).

2. Further study of British Devonian conodont faunas and correspondence with friends engaged on similar studies in other areas suggest that the presence of *Belodus* is far more widespread in the Devonian than has previously been recognized. It may ultimately prove that this genus extends into the Devonian, in which case one of the apparent anomalies of the British faunas would be explained. The occurrence of paltodids, however, may still indicate the possibility of some stratigraphic admixture, although this now appears less likely than it did before.

3. A review of distribution of other Upper Paleozoic conodont faunas in Britain is given by Dineley & Rhodes (1956).

4. Müller (1956, p. 825) has studied the type specimens of the type species of the genus *Elsonella*. His study confirms the authors' suggestion (Rhodes & Dineley, 1957, p. 361) that *E. secunda* Youngquist should be excluded from that genus. Müller's discovery of the presence of a median branch in a paratype of the type species *Elsonella prima*, has led him to redefine the genus so as to make the median branch a diagnostic character. This redefinition would exclude the specimen from Limestone 4 (Rhodes & Dineley, 1957, p. 361) which we tentatively referred to *Elsonella*.

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# DISCUSSION

S. E. Nakkady's paper *Biostratigraphy and Inter-regional Correlation of the Upper Senonian and Lower Paleocene of Egypt* (Journ. Paleont., vol. 31, p. 428–447, 1957) is misleading. His conclusions are based on two erroneous assumptions.

1. That the Danian and Montian are of different age.
2. That the Foraminifera referred to are are of Danian age.

This criticism is based primarily on the results of studies by Loeblich & Tappan on the planktonic foraminifera of the Paleocene on a world wide basis, and their conclusions, presented at the A.A.P.G. meetings in St. Louis in April, 1957.

Nakkady has assumed different ages for the Danian and Montian. Loeblich & Tappan have given excellently documented proof that the Danian and Montian are correlative and lie within their *Globigerinoides daubjergensis-Globorotalia compressa* zone.

Further use of the Danian in this discussion will imply equivalency to the Montian, unless enclosed by quotes indicating the usage of Nakkady. The Danian is considered Lower Paleocene and the Landenian Upper Paleocene.

Nakkady has placed the Kincaid formation of Texas in the Danian and the Wills Point formation in the Montian. These two formations lie within the *daubjergensis-compressa* zone and are Danian equivalents. Separation of these two formations should not be made on a time basis beyond upper and lower Danian. On the basis of this zone it is possible to correlate the following North American formations: Basal part of the Velasco of Mexico; the Midway of Texas and Arkansas; the Clayton of Missouri, Tennessee, Mississippi, Alabama (Pine Barren and McBride members), and Georgia; the basal portion of a subsurface Paleocene unit in North Carolina; the Brightseat in Maryland; and subsurface Hornerstown in New Jersey. This *daubjergensis-compressa* zone is world-wide in extent and includes the type Danian and the type Montian. Neither of these species is reported by Nakkady from his Egyptian material.

The planktonic Foraminifera reported by Nakkady from his "Danian" and "Montian" are primarily keeled *Globorotalia*. He lists *G. aequa* (Cushman & Renz), *G. angulata* (White), and *G. velascoensis* (Cushman). These species are found in Loeblich & Tappan's "keeled *Globorotalia*" zone of Landenian equivalence. In North America this includes the following formations: the upper Velasco of Mexico; the Porters Creek (Mathews Landing marl member), the Naheola (Oak Hill and Coal Bluff members), and the Salt Mountain limestone of Alabama; the upper subsurface Paleocene unit of North Carolina; the Aquia of Virginia and Maryland; and the surface Hornerstown and Vincentown of New Jersey.

Nakkady also lists *Globigerina mckannai* White (synonymous with *G. esnaensis* (LeRoy)), *G. pseudobuloides* (Plummer) and *G. triloculinoides*, the former is restricted to the Landenian and the latter two range throughout the Paleocene.

No keeled *Globorotalia* are known from the type Danian or its equivalents. Nakkady records the presence of *G. velascoensis* from the type Montian. Careful examination of the "tuffeau de Cipley" has failed to produce this species or any keeled *Globorotalia*. The presence of the keeled *Globorotalia* and the absence of *Globigerinoides daubjergensis* (Bronnimann) and *Globorotalia compressa* (Plummer) indicate the Nakkady is working with post-Danian sediments of Landenian age.

The *daubjergensis-compressa* is worldwide in occurrence and it is highly probable that Danian equivalents would be expected in the Egyptian section. Nakkady's "buffer zone" is the logical place to expect the Danian. He describes it as having "almost no *Globotruncana* or *Globorotalia*, but has a rich *Globigerina* fauna." A more detailed study of this zone on the specific level seems advisable.

This sequence of a *Globotruncana* zone below a *Globigerina* zone which in turn is overlain by a *Globorotalia* (keeled) zone is recognized throughout the world and very strikingly in the Middle East. The *Globotruncana* died out at the end of the Cretaceous, and their presence with *Globigerina* in post-Cretaceous sediments must be due to reworking. No true *Globigerina* are known from the Upper Cretaceous; also no keeled *Globorotalia* are known from below the Landenian.

Nakkady lists the following keeled forms

from his "*Globorotalia* zone: *G. angulata*, *G. crassaformis*, *G. velascoensis*, and *G. simulatilis* and states, "this fauna had its beginning in the Danian, and it has much in common with the Danian of the Caucasus, Velasco, and the type Danian." There are no keeled *Globorotalia* in the type Danian, nor in its equivalents in the Caucasus or the Velasco. The upper Velasco does contain a keeled *Globorotalia* fauna. Nakkady refers to the Velasco as Danian, which is true only of the basal portion; the upper members are Landenian. He apparently assumes a Danian age for the entire Velasco formation.

The fauna reported by Sigal (1949) from Algeria, referred to by Nakkady, is found at least as high as the Naheola formation and consequently is diagnostic to both the Danian and Landenian.

Nakkady states that *Globorotalia aequa* is known from the basal Midway. This species is not known from any of the basal Midway. Nakkady further states that the "Egyptian Danian can be readily correlated with the basal Midway." The "Danian" fauna discussed in this paper can under no circumstances be correlated with the basal Midway, nor with the "upper Midway" if reference is made to the Texas section (i.e. Wills Point formation).

Nakkady offers no valid reason for separating his "Danian" and "Montian" and further states, "the two have many important elements in common, forms which constitute the major part of the fauna." None of the benthonic species listed by Nakkady from his "Danian" and "Montian" is diagnostic of the Danian in North America. The significance of *Eponides lotus* as a "Montian" species seems invalid as this species ranges from the Danian through the Wilcox. Nakkady's breakdown into "Danian" and "Montian" faunas is meaningless and these units to which he refers are in reality younger than true Danian equivalents.

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RICHARD A. PAGE
U. S. National Museum

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# REVIEW

MISSISSIPPIAN CEPHALOPODS OF NORTHERN AND EASTERN ALASKA, Descriptions and illustrations of 43 nautiloids and ammonoids and correlation of the assemblages with European Carboniferous goniatite zones; by Mackenzie Gordon, Jr., U. S. Geol. Survey, Prof. Paper 283, 61 p., 26 text-fig., 6 pl., 1957. $1.50.

This report is a detailed account of the Early Carboniferous cephalopod faunas secured in two regions north of the Arctic Circle, in the Brooks Range, during the 1945–53 geologic exploration for the adjacent Naval Petroleum Reserve. However, it includes also a study of related materials collected long ago in the Eagle-Circle district of the upper Yukon near the Alaska-Canada boundary. All of the known occurrences of Mississippian cephalopods in Alaska are tabulated, most are shown on index maps, and their age is considered.

Altogether representatives of 12 genera of nautiloids and 14 of goniatites are illustrated and described. The nautiloids belong in well-known widely distributed Late Paleozoic genera, whereas the goniatites suggest correlations with the classic Carboniferous zones of western Europe, especially the British Isles. The latter are referred to such significant genera as *Muensteroceras* of the Early Mississippian and a number of Middle-Upper Mississippian forms: *e.g. Beyrichoceras*, *Goniatites*, *Girtyoceras*, and *Entogonites*. A good representation of American pericyclids is recorded for the first time.

The collections came from a region that is intermediate geographically between faunas known from the U.S.A. and Eastern Hemisphere, and therefore they are more than ordinarily significant. Through published lists compiled years ago by the late Geo. F. Girty, we have long been aware that Lower Carboniferous nautiloid and goniatite faunas occurred in Alaska. Now their nature is known, and students of cephalopods owe a debt of gratitude to the men who collected the materials on which this study is based, to the author of the report, and to the Geological Survey for issuing it in such a satisfactory format. Because of the value of goniatites for stratigraphic purposes, the various zones represented can be correlated with those known elsewhere.

The plates consist of photographs which are uniformly good, as are the text-figures. The latter portray the shape of the conch and the nature of the sutures in comprehensive fashion. The author has taken advantage of the unexcelled library facilities available to him and also has made direct comparisons with European and North African collections. His systematic paleontology is sound and conservative.

A. K. MILLER & W. M. FURNISH
State University of Iowa
Iowa City

# SOCIETY RECORDS AND ACTIVITIES

## SPECIAL RESOLUTION ON DEATH OF W. H. TWENHOFEL ADOPTED AT S.E.P.M. COUNCIL MEETING, MARCH 31, 1957

"A Resolution on the death of W. H. Twenhofel was read by President Shrock and it was moved, seconded, and carried that it be read to the Society Business Meeting on Tuesday."

WILLIAM HENRY TWENHOFEL, dean of American sedimentologists, child of the fossiliferous shale hills of Kentucky across the Ohio from Cincinnati, student of Schuchert and disciple of Barrell, taught thousands of students at Kansas and Wisconsin, and after retirement at Yale and the University of Tulsa, reached many more thousands through his writing, and profoundly influenced sedimentology and stratigraphy in North America for a generation.

Possessed of driving ambition, strong personal discipline, and almost incredible energy, he was a devoted scientist who, once committed, went where he needed to go, did what had to be done, and completed the assignment. His record of professional service and of published works is his monument to this devotion.

His was the creed and the attitude of a past generation. He accepted frugality as a way of life, long hours and hard work as a prerequisite of self respect, service to his profession and to his science as an inescapable responsibility, and loyalty to his friends and to truth the unquestioned obligation of man, teacher and scientist.

As scientist speaking before his peers, he commanded their respect, and meeting with them in committee he received their cooperation when it was requested, because they knew he never asked anyone to work harder or to do more than he himself was prepared to do.

He was at his best when lecturing to undergraduate students, and many a successful petroleum geologist has him to thank for a thorough grounding in the fundamentals of geology. He had deep respect for the teaching profession and a strong sense of responsibility to the student to give him the best possible training in whatever subject he happened to be teaching.

He has been a bulwark of strength in our Society since its founding. For the first two years, as one of the associate editors, he assisted Raymond C. Moore, editor, in getting the *Journal of Sedimentary Petrology* launched; then for the next eighteen he served as editor, and by the end of this score of years he had brought our Journal to the highly respected position it now holds among geological periodicals.

He was our President in 1935 and served our Society in many little noticed but highly important ways throughout his thirty years of membership. His election as Honorary Member in 1949 was recognition of his valuable services to our Society as well as of his distinguished contributions to our fields of interest.

His was a full, active and healthy life, intensely devoted to teaching, investigating and writing. Death came quickly and gently at forescore years and one to end the work of a great American student of sediments and sedimentary rocks.

Therefore Be It Resolved: That the Society of Economic Paleontologists and Mineralogists, in recognition of the great loss it has sustained, record in the minutes of this meeting its tribute to William Henry Twenhofel and its appreciation of his long and distinguished service to this Society in particular and to geology in general.

## ANNOUNCEMENT OF MEETING

Annual Technical Meeting of the Society of Economic Paleontologists and Mineralogists (Permian Basin Section) will be held in Midland, Texas, on March 27, 28, and 29, 1958. Registration and sessions will be at the Hotel Scharbauer.

W. A. Waldschmidt, 311 Leggett Building, Midland, Texas, is president of the Permian Basin Section; and D. A. Zimmerman, 503 North Central Expressway, Richardson, Texas, will head the Technical Program Committee.

This announcement is made in the hope that serious conflicts with other meetings can be avoided on this date.

JOSEPH P. D. HULL, JR.
Box 1600
Midland, Texas

JOURNAL OF PALEONTOLOGY, VOL. 31, NO. 6, P. 1180–1183, NOVEMBER 1957

# ZOOLOGICAL NOMENCLATURE

## PROPOSED ADDITION TO THE "REGLES" OF PROVISIONS RECOGNISING AND REGULATING THE NOMENCLATURE OF "PARATAXA"

Plan submitted jointly by RAYMOND C. MOORE (*University of Kansas, Lawrence, U.S.A.*) and P. C. SYLVESTER-BRADLEY (*University of Sheffield, England.*)

*Request to specialist bodies and specialists for advice*

(Note by the Secretary to the International Commission on Zoological Nomenclature.)

Arrangements have been made by the International Trust for Zoological Nomenclature for the publication at a very early date in the special London Congress (1958) Agenda Volume of the *Bulletin of Zoological Nomenclature* (Volume 15, Part 1/3) of a group of three papers written jointly by Professor Raymond C. Moore (*University of Kansas, Lawrence, Kansas, U.S.A.*) and P. C. Sylvester-Bradley (*University of Sheffield, England*) containing proposals for the incorporation in the International Code of Zoological Nomenclature of a group of provisions recognising and defining the concept "parataxon" and providing for the regulation of the nomenclature of units belonging to this category.

2. In view of the novelty of the proposed plan and the inevitable complexities involved it is evident that the Fifteenth International Congress of Zoology when it meets in London in 1958 is likely to wish to satisfy itself not only that the proposals are well-conceived but also that they command a representative body of support among palaeontologists. This is all the more important in the present case in view of the fact that its subject is primarily of interest to palaeontologists, a body of specialists who are normally not strongly represented at International Congresses of Zoology. In these circumstances consideration has been given by Professor Moore and myself to the question of the procedure to be adopted for bringing the foregoing proposals prominently to the attention of interested specialists in advance of the London Congress.

3. It is to be hoped that in part the foregoing object will be achieved by the publication in the *Bulletin of Zoological Nomenclature* of the detailed papers prepared by the applicants and also by the issue of Public Notices to representative serial publications at the time when these applications are published in the *Bulletin*. Experience has shown however that in the case of exceptionally complicated problems and also in that of cases of a general—as contrasted with a specialised—interest the foregoing procedure is not always capable of securing as fully a representative sample of comments as is desired. This problem arose in 1952 in connection with proposals affecting certain broad issues touching the provisions of the *Regles*. It was then decided that the normal methods for obtaining the views of interested specialists should be supplemented by the distribution of questionnaires to specialist bodies and individual specialists. The replies to these questionnaires were published in the special Copenhagen (Congress, 1953) Agenda volumes of the *Bulletin* (Volumes 8 and 10) immediately upon their receipt in the Office of the Commission. It has been decided to adopt a similar procedure in the present case.

4. In pursuance of the foregoing decision Professor Moore has kindly prepared a digest of the lengthy documents in which he and Mr. Sylvester-Bradley had discussed the problem of the nomenclature of parataxa, in which he drew attention to the principal issues involved and gave particulars of the provisions which it was recommended should be inserted in the *Regles*. The digest so prepared by Professor Moore is attached to the present note as an Annexe.

5. It is particularly hoped that the specialist bodies and individual specialists to whom the present document is being despatched will be so good as to assist the International Commission on Zoological Nomenclature and, through it, the Fifteenth International Congress of Zoology, London, 1958, by communicating statements to this Office:

(1) setting out their views on the proposals submitted by Professor

Moore and Mr. Sylvester-Bradley;

(2) indicating, if they consider that those proposals ought to be expanded or otherwise amended in any respect, how the changes desired should be fitted into the general framework of the plan submitted in this case.

6. *Answers to the present appeal for advice should be addressed to the Secretary, International Commission on Zoological Nomenclature (address: 28, Park Village East, Regent's Park, London N.W.1.).* Communications so received will be published in the Agenda volume of the *Bulletin of Zoological Nomenclature* immediately upon their being received. In view of the importance attached to the early publication in the above volume of the *Bulletin* of comments on all matters of nomenclature to be brought before the London Congress next year, it will be particularly appreciated if recipients of the present request for assistance will be so kind as to furnish replies at the earliest date which they may find to be practicable.

(sgd.) FRANCIS HEMMING
*Secretary to the International Commission on Zoological Nomenclature.*

*4th July, 1957.*

## ANNEXE

Digest of an application submitted by R. C. Moore and P. C. Sylvester-Bradley for the introduction into the "Regles" of provisions recognising parataxa as constituting a special category for the classification and naming of Discrete Parts or Life-Stages of Animals which are inadequate for identification as Whole-Animal Taxa

*Digest prepared by Raymond C. Moore (University of Kansas, Lawrence, Kansas, U.S.A.)*

The purpose of applications proposing recognition of classificatory units termed "parataxa" is to remove instability and confusion affecting the nomenclature of several thousand kinds of already named Discrete Parts of animals (almost exclusively fossils) which are unidentifiable as belonging to generic and specific taxa of Whole Animals or are even unplaceable in suprageneric taxa. A large majority of these fragmentary remains have been demonstrated to possess high value in stratigraphic paleontology. Similarly, certain life-stages of parasites, very important in medical studies, are indeterminable as to the taxa of adults and possibly these may be usefully defined as parataxa.

2. As a basic premise we may agree that zoological taxonomy comprises a single system based on presumed natural relationships and into this system all animals, with varying degree of success, may be fitted. However, because many Discrete Parts of animals cannot be incorporated in any Whole-Animal taxa, a system of parataxonomy that is measurably independent of zoological taxonomy is called for. Then classification and nomenclature applicable to the Discrete Parts of unidentified animals may proceed without confusion or disturbance of either category (taxa or parataxa) with the other. It is needful that all rules governing nomenclature of whole-animal taxa should be applied without any difference in mode or force to the category of parataxa as used for Discrete Parts of unidentifiable Whole Animals, except that for purposes of the Law of Priority a wall should be conceived to separate nomenclature of Whole-Animal taxa from nomenclature of parts defined as parataxa. For the purposes of the Law of Homonymy, taxa and parataxa would be coordinate.

3. Names given to Discrete Animal parts representing unknown Whole-Animal taxa have been treated in three different ways, none of them satisfactory. All consist of binomina for "specific" units and trinomina for "subspecific" units.

(a) Names construed to differ in no way from those employed for Whole-Animal taxa and conforming to Article 27 (a) of the *Regles* which stipulates that "the oldest available name is retained when any part of the animal is named before the animal itself;"

(b) Names construed as "technical terms" (Paris, 1948) which are rejected from the domain of zoological nomenclature; and

(c) Names construed to designate "form" taxa analogous to "form-genera,"

"organ-genera," "form-species," etc., of the Botanical Code but not recognised by zoological rules.

4. If nomenclature of Discrete Animal parts is governed exactly in the manner accepted for naming of Whole Animals (see paragraph 3 [a] above), there would be a continuous risk of confusion and instability of nomenclature which may be serious. Out of many examples, two are cited briefly here.

(a) *Trigonellites lamellosus* Parkinson, 1811, based on an ammonoid aptychus (operculum) is the type species of *Trigonellites* Parkinson, 1811. It was described from a specimen not associated with a conch. Subsequently, *T. lamellosus* has been found *in situ* within conchs identified as *Oppelia flexuosa* (von Buch, 1831); *O. discus* (Quenstedt, 1856); and *O. euglypta* (Oppel, 1863). The genus *Oppelia* Waagen, 1869, is based on *Ammonites subradiatus* Sowerby, (J. de C.), 1823, as type species, described from a conch. If *Trigonellites* and *Oppelia* are correlative competing names, Article 27 (a) would call for the acceptance of *Trigonellites* and the rejection of *Oppelia*, despite very long and widespread use of *Oppelia* for scores of species, including fossil zone guide forms. Also, it would be inadmissable for three valid species as defined by conchs (*O. flexuosa; O. discus;* and *O. euglypta*) to be synonymized under the name *Trigonellites lamellosus*.

(b) A Whole-Animal (?) species named *Scottognathus typicus* (Rhodes, 1952) is based on 132 natural assemblages of Pennsylvanian (Upper Carboniferous) conodonts. *Scottognathus* Rhodes, 1953, is a substitute name for *Scottella* Rhodes, 1952 (*nec* Enderlein, 1910). Discrete components of these assemblages are conodonts named *Hindeodella delicatula* Stauffer & Plummer, 1932; *Synprioniodina microdenta* Ellison, 1941; *Idiognathodus claviformis* Gunnell, 1931; *Streptognathodus excelsus* Stauffer & Plummer, 1932; and *Ozarkodina delicatula* Stauffer & Plummer, 1932. Generic synonymy of *Scottognathus* & of one or more of its constituents can be established only if the type species of discrete conodont genera recognized in the assemblages is present. *Hindeodella* and *Synprioniodina*, Bassler, 1925, and *Ozarkodina* Branson & Mehl, 1933, are not represented by their type species, whereas *Idiognathodus* Gunnell, 1931, and *Streptognathodus* Stauffer & Plummer, 1932 are represented by their type species. Accordingly, under Article 27, *Scottognathus typicus* must yield to *Idiognathodus claviformis* as the name for the assemblage. Out of sixty-four nominal species of *Idiognathodus* and forty-three of *Streptognathodus*, all but thirty-one are listed as synonyms of discrete conodonts found in such association with "*Scottognathus typicus*" as to indicate that they have been derived from animals conspecific with this species. It is difficult indeed to see by what names these forms should be described under the present *Regles*.

5. Names treated as "technical terms" which are expressly rejected as zoological names lack government by the Laws of Homonymy and Priority, as well as other regulation, thus promoting chaos in nomenclature. Virtually all names published for parts of unidentified whole animals are binomina composed of "generic" and "specific" Latinized names exactly similar to zoological names and because most fossils are varyingly incomplete, discrimination between those considered suitable for nomenclature under zoological rules and those excluded from such treatment is wholly subjective. Indeed, the probably complete skeletal remains of some organisms assignable to protistan groups have been named by Deflandre using intended "Technical term" procedure whereas most authors would consider the published names (without regard to intent of the author) as undeniably acceptable zoological names. Here lies confusion.

6. The concepts of "form-genera" and "form-species" might be adapted advantageously to classification and nomenclature of

Discrete Parts of unidentified animals but they contravene the rules of zoological nomenclature. It seems preferable to recognize a special category of "associate taxa," that is, parataxa, which would be correlative with all zoological names for the purposes of the Law of Homonymy but would constitute a wholly segregated group for purposes of the Law of Priority. In this way instability and confusion of nomenclature would be easily avoided. In order to avoid subjective variation in deciding what zoological objects are to be classified and named in terms of parataxa, rather than in those of whole-animal taxa, it is recommended that this be determined solely by the Commission.

7. Recommendation is made accordingly:

(i) that Article 27 (a) should be modified by adding the phrase "except for parataxa," thus excluding the classificatory units called parataxa from application of the Article: and

(ii) that a new Article should be incorporated in the *Regles:*

(a) defining "parataxon" as a taxonomic category comprising Discrete Parts or Life-Stages of animals, which, by decision of the Commission, are deemed to be unidentifiable in terms of the whole animals that produced them;

(b) stipulating that classification and nomenclature of any group of Discrete Parts or Life-Stages of animals in terms of parataxa shall be allowed only after the Commission has ruled to this effect and then such ruling shall apply retroactively irrespective of whether an author uses the term "parataxa"; and

(c) providing that the nomenclature applied to taxa and parataxa shall be mutually exclusive and independent for the purposes of the Law of Priority, but coordinate for the purposes of the Law of Homonymy, names belonging to one category not being transferable to the other.

NOTE 1. It should be noted here that in 1954 Dr. W. J. Arkell made an application to the International Commission for the grant of a *Declaration* excluding from availability for the purposes of zoological nomenclature, i.e. for the purposes of what Professor Moore here terms the nomenclature of "whole-animal taxa" of any name based solely upon the Aptychus of an ammonite and proposing the addition to the *Official Indexes of Rejected and Invalid Names* of a number of such names, including the name *Trigonellites* Parkinson, 1811, here cited by Professor Moore as an example (Arkell [W.J.], *Bull. Zool. Nomencl.* 9: 266–269). No action has as yet been taken by the International Commission on the above application, it having been considered better to defer action thereon until a decision had been taken by the International Congress of Zoology on the wider issues of a general character which it was known that Professor Moore and Mr. P. C. Sylvester-Bradley proposed to raise, i.e. the proposals put forward in the papers, of which Professor Moore has here given a digest. (Initialled F.H. 4th July, 1957.)

NOTE 2. The complete text of the Moore and Sylvester-Bradley proposal and other pertinent documents are published in Volume 15 of the *Bulletin of Zoological Nomenclature.*

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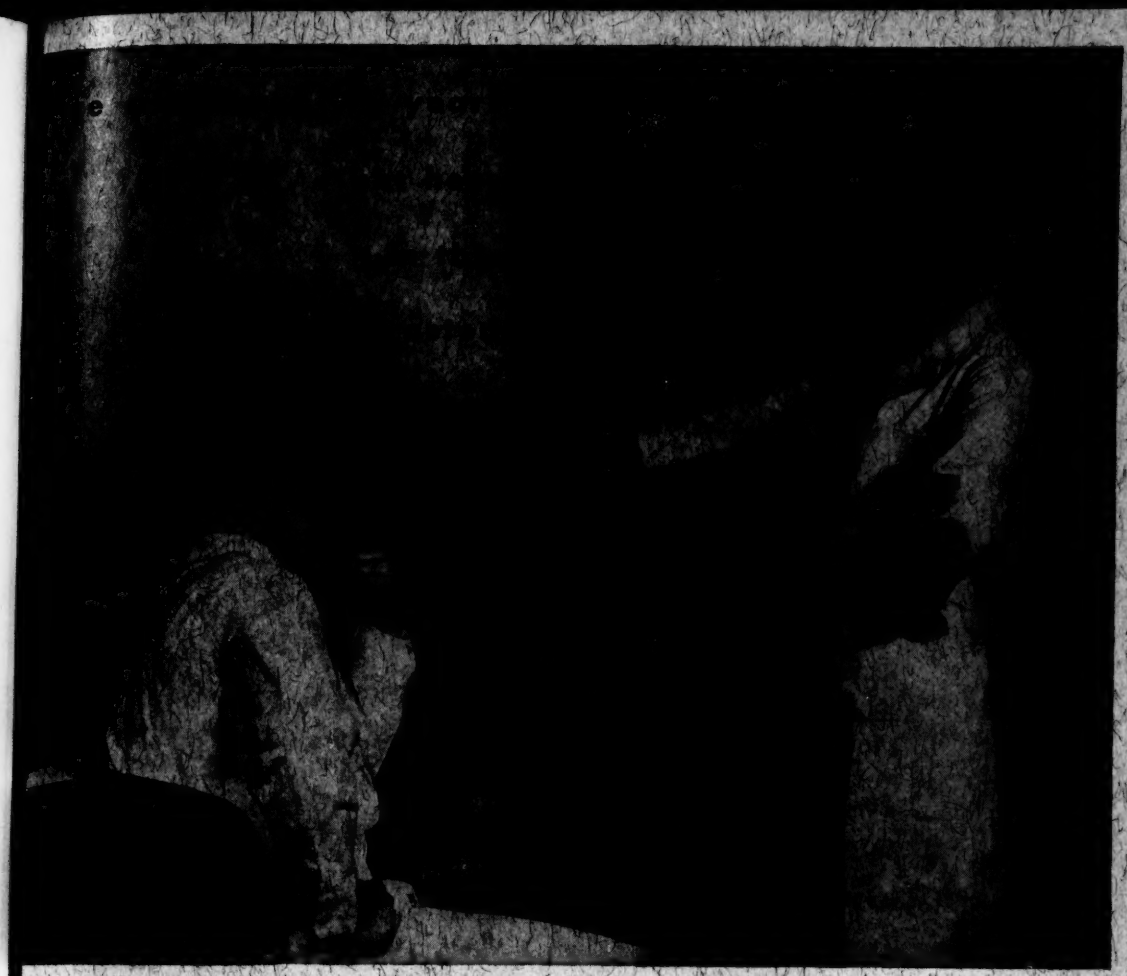

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